

TROPHIC ROLES OF JUVENILE PENAEUS AZTECUS IVES AND
PENAEUS SETIFERUS (LINNAEUS) IN A TEXAS SALT MARSH

A Dissertation

by

TERESA ANN MCTIGUE

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of
DOCTOR OF PHILOSOPHY

August 1993

Major Subject: Wildlife and Fisheries Sciences

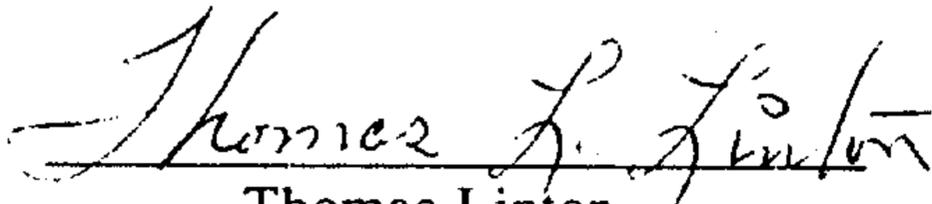
TROPHIC ROLES OF JUVENILE PENAEUS AZTECUS IVES AND
PENAEUS SETIFERUS (LINNAEUS) IN A TEXAS SALT MARSH

A Dissertation

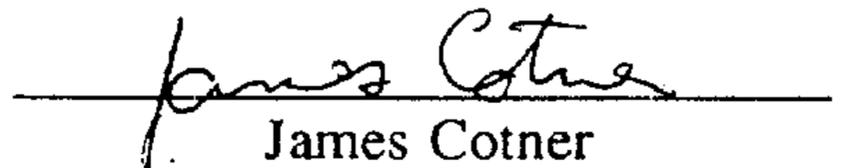
by

TERESA ANN MCTIGUE

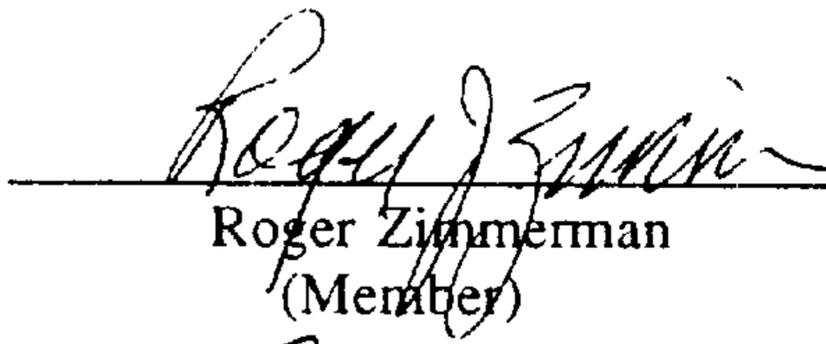
Approved as to style and content by:



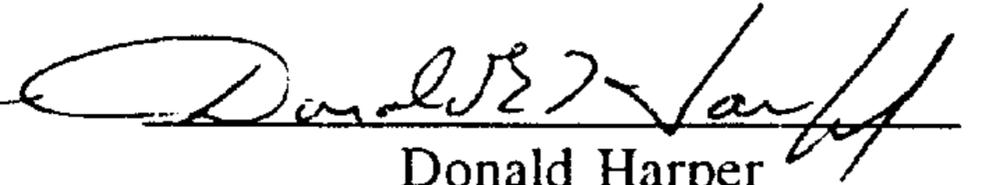
Thomas Linton
(Co-chair of Committee)



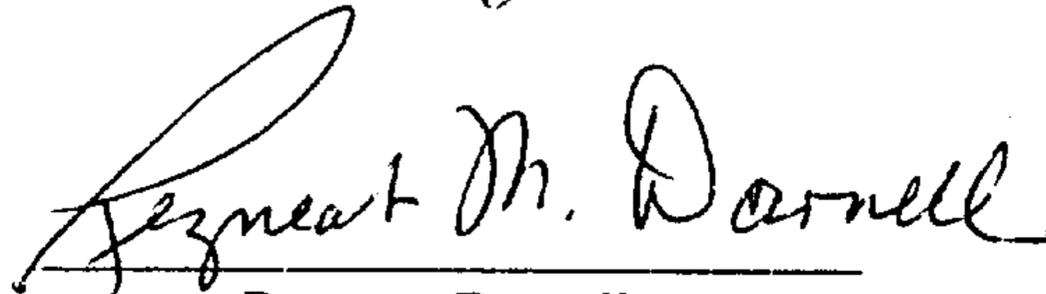
James Cotner
(Co-chair of Committee)



Roger Zimmerman
(Member)



Donald Harper
(Member)



Rezneat Darnell
(Member)



Robert Brown
(Head of Department)

August, 1993

ABSTRACT

Trophic Roles of Juvenile Penaeus aztecus Ives and Penaeus setiferus (Linnaeus) in a Texas Salt Marsh. (August, 1993)

Teresa Ann McTigue, B.S., University of Maryland;

M.S., University of South Carolina

Co-Chairs of Advisory Committee: Dr. Thomas Linton
Dr. James Cotner

Penaeus aztecus Ives, the brown shrimp, and Penaeus setiferus (Linnaeus), the white shrimp, co-occur in Texas salt marshes as juveniles. While their basic life cycles are similar, evidence indicates that the species utilize different resources for the primary faunal element of their diets. Through prey selection and growth studies, brown shrimp were shown to successfully remove infauna from natural sediment. Further, a diet of polychaetes, whether alone or in combination with algae, produced growth in the species. By contrast, white shrimp neither removed infauna nor grew to a significant degree when provided polychaetes or amphipods as food. A predator-exclusion caging study suggested that brown shrimp may significantly affect polychaete populations in marsh areas, but their impact on amphipods or any taxon living in open bay bottom is not clear and may be much less. Pressures defining infaunal populations may vary with habitat and group of animal considered. Brown shrimp appear to be trophically linked to infaunal populations. The

structure and dynamics of the benthic community may to directly affect local penaeid productivity. Areas dominated by surface dwelling polychaetes as opposed to deep burrowers may provide more accessible foraging for juvenile brown shrimp. White shrimp are omnivorous as well, but do not rely on infaunal material to the same extent as the brown shrimp. The primary faunal element in the diet of white shrimp has not yet been identified. The dietary differences between the two species may play a role in defining which species dominates in regions with varying marsh accessibility. While prey choice and availability are not the only factors influencing penaeids, they may greatly affect production and local success of populations.

ABSTRACT

Trophic Roles of Juvenile Penaeus aztecus Ives and Penaeus setiferus (Linnaeus) in a Texas Salt Marsh. (August, 1993)

Teresa Ann McTigue, B.S., University of Maryland;

M.S., University of South Carolina

Co-Chairs of Advisory Committee: Dr. Thomas Linton
Dr. James Cotner

Penaeus aztecus Ives, the brown shrimp, and Penaeus setiferus (Linnaeus), the white shrimp, co-occur in Texas salt marshes as juveniles. While their basic life cycles are similar, evidence indicates that the species utilize different resources for the primary faunal element of their diets. Through prey selection and growth studies, brown shrimp were shown to successfully remove infauna from natural sediment. Further, a diet of polychaetes, whether alone or in combination with algae, produced growth in the species. By contrast, white shrimp neither removed infauna nor grew to a significant degree when provided polychaetes or amphipods as food. A predator-exclusion caging study suggested that brown shrimp may significantly affect polychaete populations in marsh areas, but their impact on amphipods or any taxon living in open bay bottom is not clear and may be much less. Pressures defining infaunal populations may vary with habitat and group of animal considered. Brown shrimp appear to be trophically linked to infaunal populations. The

structure and dynamics of the benthic community may to directly affect local penaeid productivity. Areas dominated by surface dwelling polychaetes as opposed to deep burrowers may provide more accessible foraging for juvenile brown shrimp. White shrimp are omnivorous as well, but do not rely on infaunal material to the same extent as the brown shrimp. The primary faunal element in the diet of white shrimp has not yet been identified. The dietary differences between the two species may play a role in defining which species dominates in regions with varying marsh accessibility. While prey choice and availability are not the only factors influencing penaeids, they may greatly affect production and local success of populations.

ACKNOWLEDGMENTS

I would like to express my gratitude to Dr. Thomas Linton and Dr. James Cotner, the co-chairmen of my committee. Dr. David Aldrich, co-chair until his retirement, contributed to my success as well. My committee members, Dr. Rezneat Darnell, Dr. Donald Harper, and Dr. Roger Zimmerman, were patient and always available to assist me. I owe them each thanks. This dissertation would not have been completed without the volunteer labor of many Texas A&M University at Galveston undergraduates. This long list includes Raymond Burditt, Jill Grafton, Shannon Whaley, Stephanie Jones, Bill Watson, Daniella Palluzzi, David Carter, Jeff Davis, Kelley Parker, Grant Sybrant, Jeff Rodack, Mark Reihling and Ken Osborne. If I inadvertently forgot anyone, I am sorry. These cheerful individuals assisted in all aspects of lab and field work and generally made my life much easier. My parents, William and Bernice McTigue, in addition to supporting me, also assisted with field work when they were in Galveston. Finally, I am indebted to the Dr. Edward Klima, past director, and Dr. Roger Zimmerman, acting director, and the staff of the National Marine Fisheries Service's Galveston Laboratory for supporting my research and employing me through the great majority of my dissertation work. Special thanks go to Dr. Thomas Minello, Zoula Zein-Eldin, and Dr. Daniel Childers for discussing matters of statistics and ecology at length with me.

TABLE OF CONTENTS

	Page
ABSTRACT.....	iii
ACKNOWLEDGMENTS.....	v
LIST OF TABLES	vii
LIST OF FIGURES	x
INTRODUCTION	1
METHODS.....	1 3
Infaunal Removal Experiment.....	1 3
Growth Experiment.....	1 4
Predator Exclusion Study.....	1 6
RESULTS.....	2 0
Infaunal Removal Experiment.....	2 0
Growth Experiment.....	3 1
Predator Exclusion Study.....	4 8
DISCUSSION.....	6 8
CONCLUSIONS	8 7
REFERENCES	9 1
VITA	1 0 2

LIST OF TABLES

	Page
Table 1. Results of t-tests comparing infaunal organismal abundances between control cores of sediment and those in which brown shrimp had fed for four days.....	2 1
Table 2. Results of t-tests comparing control cores to those in which brown shrimp fed for four days.....	2 2
Table 3. Results of t-tests comparing infaunal organismal abundances between control cores of sediment and those in which white shrimp had fed for four days.....	2 6
Table 4. Results of t-tests comparing control cores to those in which white shrimp fed for four days.....	2 7
Table 5. Analysis of variance of survival of brown and white shrimp fed experimental diets.....	3 3
Table 6. Contrasts performed on shrimp survival data within and between species of shrimp.....	3 4
Table 7. ANOVA contrast procedure performed on shrimp survival data for brown shrimp.....	3 5
Table 8. ANOVA contrast procedures performed on shrimp survival data for white shrimp.....	3 6
Table 9. Repeated measures analysis of variance (ANOVA) of incremental growth of brown and white shrimp fed experiment diets.....	3 7
Table 10. Repeated measures analysis of variance (ANOVA) of incremental growth of brown and white shrimp fed experiment diets.....	3 8
Table 11. Contrasts associated with ANOVA procedures performed on shrimp incremental growth data within and between species of shrimp including polychaete, amphipod, polychaete + Skeletonema, and amphipod + Skeletonema diets.....	3 9

	Page
Table 12. Contrasts performed during ANOVA procedures on brown shrimp incremental growth data including polychaete, amphipod, polychaete + Skeletonema, and amphipod + Skeletonema diets.....	4 3
Table 13. Contrasts performed during ANOVA procedures on white shrimp incremental growth including polychaete, amphipod, polychaete + Skeletonema, and amphipod + Skeletonema diets.....	4 6
Table 14. Calculation of removal rate of polychaetes per day by brown shrimp using natural densities from a surface area of 78.5 cm ² representing the coring device used in sampling.....	5 0
Table 15. Calculation of removal rate of amphipods per day by natural densities of brown shrimp from a surface area of 78.5 cm ² representing the coring device used in sampling.....	5 1
Table 16. Description of formula and definition of terms used in calculation of theoretical effects of juvenile brown shrimp feeding on infauna in the absence of other predators.....	5 2
Table 17. Results of repeated measures analysis of variance (ANOVA) comparing the change in the dry weight of polychaetes in vegetated areas among natural cores of sediment, cores from inside predator exclusion cages, and a theoretical line predicting the effects of the feeding of brown shrimp alone.....	5 3
Table 18. Results of repeated measures analysis of variance (ANOVA) comparing the change in the dry weight of amphipods in vegetated areas among natural cores of sediment, cores from inside predator exclusion cages, and a theoretical line predicting the effects of the feeding of brown shrimp alone.....	5 5

Table 19. Contrasts constructed from ANOVA procedures comparing levels of amphipod biomass (dry weight per experimental core) between predation treatments in vegetated marsh areas.....	56
Table 20. Results of repeated measures analysis of variance (ANOVA) comparing the change in the dry weight of polychaetes in unvegetated areas among natural cores of sediment, cores from inside predator exclusion cages, and a theoretical line predicting the effects of the feeding of brown shrimp alone.....	58
Table 21. Contrasts constructed from ANOVA procedures comparing levels of polychaete biomass (dry weight per experimental core) between predation treatments in nonvegetated areas.....	59
Table 22. Results of repeated measures analysis of variance (ANOVA) comparing the change in the dry weight of amphipods in unvegetated areas among natural cores of sediment, cores from inside predator exclusion cages, and a theoretical line predicting the effects of the feeding of brown shrimp alone.....	61
Table 23. Abundances of dominant species of polychaetes and amphipods collected in cores (78.5 cm ²) from inside predator exclusion cages (no predation) and outside the cages (natural predation).....	63

LIST OF FIGURES

	Page
Figure 1. A comparison of infaunal densities between control cores and cores in which penaeid shrimp have fed for four days.....	23
Figure 2. Depletion of infauna in cores (78.54 cm ²) in which brown shrimp were held for four days beginning February 23, 1990.....	24
Figure 3. Depletion of infauna in cores (78.54 cm ²) with brown shrimp over four days beginning May 31, 1990.....	25
Figure 4. Depletion of infauna from cores of sediment (area = 78.54 cm ²) in which white shrimp were placed for four days beginning August 10, 1990.....	28
Figure 5. Depletion of infauna from cores (area = 78.54 cm ²) in which white shrimp were held for four days beginning October 29, 1990.....	29
Figure 6. Weight change for brown and white shrimp during a four day exposure to cores of natural sediment.....	30
Figure 7. Number of days brown and white shrimp survived in experimental containers when fed the following treatment diets.....	32
Figure 8. Change in weight for brown shrimp and white shrimp fed amphipod and polychaete diets during 5 day periods over 30 days.....	41
Figure 9. A comparison of weight change for brown shrimp and white shrimp fed combination diets during 5 day periods over 30 days.....	42
Figure 10. Change in weight over 5 day periods for brown shrimp fed experimental diets of salt marsh infaunal organisms and the diatom <i>Skeletonema</i>	44

Figure 11. Change in weight over 5 day periods for white shrimp fed experimental diets of salt marsh infaunal organisms.....	45
Figure 12. Average consumption of prey items by white and brown shrimp over a five day period.....	47
Figure 13. A comparison of change in polychaete biomass (dry weight) per experimental core (78.5 cm ²) over time for three predation treatments in vegetated marsh areas.....	54
Figure 14. A comparison of change in amphipod biomass (dry weight) per experimental core (78.5 cm ²) over time for three predation treatments in vegetated marsh areas.....	57
Figure 15. A comparison of change in polychaete biomass (dry weight) per experimental core (78.5 cm ²) over time for three predation treatments in open water areas.....	60
Figure 16. A comparison of change in amphipod biomass (dry weight) per experimental core (78.5 cm ²) over time for three predation treatments in open water areas.....	62
Figure 17. A comparison of numerically dominant polychaete species inside and outside predator exclusion cages constructed on the marsh surface.....	64
Figure 18. A comparison of numerically dominant amphipod species inside and outside predator exclusion cages constructed on the marsh surface.....	65
Figure 19. A comparison of numerically dominant polychaete species inside and outside predator exclusion cages constructed over unvegetated bottom.....	66

Figure 20. A comparison of numerically dominant
amphipod species inside and outside predator
exclusion cages constructed over unvegetated
bottom.....67

INTRODUCTION

Salt marshes cover great expanses of the coastal eastern United States, from the southeastern Atlantic to the Gulf of Mexico. They are recognized for the presence of cordgrass (Spartina spp.), but with the potential for significant differences between sites (Wiegert and Freeman 1990). Within a marsh, factors such as salinity, water level, and temperature can vary drastically both daily and seasonally. Organisms residing within the area must be more tolerant of change than their offshore relatives (Teal 1962). Salt marshes are typically stable in terms of their community structure, having a low diversity of species with broad diets (Teal 1962). The organisms that are successful at exploitation of the habitat tend to be found in great densities (Biggs and Cronin 1981). Seasonally, a salt marsh community is made up of both resident and transient species and can be linked with the lifecycles of many estuarine and marine animals. Juvenile fish and crustaceans whose adult forms occur elsewhere seasonally dominate marsh areas in terms of abundance. This habitat utilization has been indicated as an important avenue of transport of materials between estuarine and near shore waters.

What is it about marshes that result in the high degree of utilization by transient juveniles? It has been postulated that marshes serve as nursery areas, decreasing the threat of

This dissertation follows the format of the journal *Estuaries*.

predation and providing an ample supply of food for the young animals (Turner, 1977; Weinstein 1979; Boesch and Turner 1984; Currin et al. 1984). The physical structure of Spartina and other typical marsh vegetation decrease the efficiency of predators by limiting their line of sight (Minello and Zimmerman 1983; Minello et al. 1989). While the benefits of reduction in predation pressure are understood, the potential food resources the juveniles are utilizing in marshes are less clear.

It is thought that there are two predominant bases to food webs within marshes (Wiegert and Freeman 1990). These are the utilization of dead particulate and dissolved organic material (POM and DOM) and benthic algae-phytoplankton production. The importance of detritus to marsh food webs has been implied through its great abundance in nature and occurrence of material identified as detritus in the guts of animals (Darnell 1961; Teal 1962; Darnell 1967; Odum and de la Cruz, 1967). Evidence from gut content analysis may be misleading, however, because modification through digestion can result in the misidentification of materials. It has become apparent that the source of particulate material is highly variable, depending on the estuary in question (Haines 1977, 1979; Haines and Montague 1979; Hackney and Haines 1980; Hughes and Sherr 1983; Fry and Sherr 1984). Further, its utilization is inconstant even within species (Fry and Sherr 1984). Despite this, particulate organic material may remain an important food source for smaller animals, such as deposit feeding polychaetes (Fauchald and Jumars, 1979).

Dissolved organic material, included by some definitions as detritus, leaches out of living and dead plant material (Turner 1978; Mann 1988). Other contributions come from the 'sloppy' feeding by animals. The leachates are known to form aggregates and may be consumed by particulate-feeding organisms (Camilleri and Ribí 1986). Detritus for many years was assumed to be the dominant energy source utilized by marsh animals. Recently, though, the role of phytoplankton, epiphytes, and edaphic algae has been realized to have potentially equal influence with the detrital complex (Sullivan and Moncreiff 1987, 1990).

The methods may vary through which the production discussed above is transferred to subsequent elements of local food webs. In polyhaline salt marshes of the Galveston Bay system, macroinfaunal communities tend to be dominated by polychaetes and amphipods (Zimmerman *et al.* 1990). These infauna make use of both trophic pathways mentioned above (Fauchald and Jumars 1979; R. Zimmerman pers. comm.) and may be important in the diets of organisms that browse along the sediment surface or deposit feed. Galveston Bay is a microtidal system that experiences long term flooding of extensive areas of marsh. Predators of infauna seasonally have extended opportunities to forage in areas densely populated by their preferred prey items. In such areas, infauna may constitute an important linkage in the energy flow within the system.

Penaeus aztecus Ives and Penaeus setiferus (Linnaeus), the brown and white shrimp, are both seasonally present in Texas salt

marshes as juveniles. During the summer and fall months, shrimp can be one of the most abundant species and are known to be preyed upon by many fish (Gunter 1945; Darnell 1958; see Minello and Zimmerman 1983 for review). Shrimp walk along surfaces probing and handling items they encounter (Dall et al. 1990). Frequently, this material is brought to the shrimp's mouthparts. It seems reasonable to suggest that prey available from the substrate, such as benthic invertebrates, could constitute an element of the diet of P. aztecus and P. setiferus. There exist, however, differences in the life histories of these animals to indicate variance in their habits.

Juvenile P. setiferus and P. aztecus are common residents of Gulf of Mexico and southeastern US Atlantic salt marsh systems. The adults of these species broadcast their eggs offshore and the subsequent larval stages are planktonic. At the postlarval stage, the shrimp invade estuaries, possibly using landward moving water masses and currents. Within the estuarine areas, penaeids live predominantly as epibenthic organisms. After two to three months, the subadult shrimp return to offshore waters (Farfante 1969; Copeland and Bechtel 1974; Weinstein 1979; Williams 1984). In the Gulf of Mexico, salt marshes serve as one of the primary nursery habitats of juvenile white and brown shrimp during their estuarine residence period (Zimmerman and Minello 1984). As is consistent with nursery function, marshes provide young penaeid shrimp refuge that reduces levels of predation (Minello and Zimmerman 1983; Minello et al. 1989). The

advantages of marsh habitat as feeding grounds for shrimp, another component of the nursery function, are not evident because so little is known of their natural dietary habits.

In the western Gulf of Mexico, Penaeus species follow the same general life cycle, although their time of immigration into estuaries differs. The brown shrimp, Penaeus aztecus, is an early spring arrival, first appearing as postlarvae in marshes from late February to early April. The white shrimp, Penaeus setiferus, do not appear until late May or June (Pearson 1939; Williams 1955; Baxter and Renfro 1966; Farfante 1969; Copeland and Bechtel 1974; Williams 1984).

Salt marshes change in several ways during the interval between peaks in immigration. Benthic infauna and epifauna reach their maximum seasonal abundance during the early spring (March) and decline rapidly after the arrival of seasonal predators (Cammen 1979; Nelson 1979a; Alon and Stancyk 1982; Kneib and Stiven 1982; Coull and Palmer 1984; Kneib 1984; Coull 1985; Flint and Kalke 1985; Zimmerman et al. 1990). By contrast, edaphic algae, evidenced in Mississippi and Delaware salt marshes, exhibit highest levels of production during the spring and summer, declining during the fall and winter (Gallagher 1971; Sullivan and Moncreiff 1987). In Georgia salt marshes, Pomeroy (1959) measured near constant rates of algal production throughout the year. Thus, algae may be present for consumption regardless of the month. In addition, the marsh tends to be warmer, with

higher salinities and lower water levels in summer compared to the spring.

Penaeid shrimp are thought to utilize the most abundant food sources present in marshes, but their diets are still not well defined. Feeding habits of the animals are difficult to determine in part because identification of gut content material is hampered by the digestive process. The mouth parts and gastric mill of the shrimp shred and grind their food producing a paste of unrecognizable, partially digested material. Identification is only possible for the few isolated hard parts or material that was quite recently consumed. Brown and white shrimp have been classified as bottom feeders who consume any available organic material (Williams 1955; Young 1959; Darnell 1961). Further research, however, indicated the penaeids to be more selective feeders than previously thought (Karim 1970; Condrey et al. 1972; Gleason and Zimmerman 1984).

Postlarval and juvenile P. aztecus are omnivorous, but the relationship between animal and plant material in their diets may change with ontogeny (Venkataramiah et al. 1975). Brown shrimp postlarvae < 25 mm in total length (TL) and young juveniles up to 44 mm TL have been described as true omnivores (Jones 1973; Gleason and Wellington 1988), although the definition of the term is somewhat unclear. The smallest juveniles are thought to feed on benthic microflora and microfauna, while older, larger juveniles, 45 - 64 mm TL, switch to macrofauna associated with sediments and plant detritus (Jones 1973). The

change from micro- to macrofauna probably is gradual and actually begins to occur well before the animals reach 45 mm in length. P. aztecus > 65 mm in total length were thought to be mainly carnivorous (Jones 1973). Using immunological techniques, Hunter and Feller (1987) confirmed the carnivorous element in the diet of brown shrimp (8 mm - 40 mm in total length), but they did not find that dietary choices of the organisms changed over time.

Brown shrimp consume animal material and grow when fed laboratory diets (Zein-Eldin 1963; Shewbart et al. 1973; Hunter and Feller 1987; McTigue and Zimmerman 1991). Growth success from consumption of plants depends on the species consumed. Flagellated algae, such as Isochrysis, produced no growth in brown shrimp (Gleason and Zimmerman 1984). This may result from the shrimp's difficulty in obtaining enough of these small algae. Postlarval brown shrimp fed plant-based diets grew more rapidly when fed the diatom Skeletonema (Cook and Murphy 1969; Gleason and Zimmerman 1984) and diatoms are an important food source for the animals (Gleason 1986). This may be because diatoms tend to settle on to surfaces and are more readily obtained by the penaeid. Brown shrimp may consume planktonic algae in addition to benthic and epiphytic forms (Gleason and Wellington 1988), although they are not known as filter feeders. By contrast, there is no good evidence that Spartina alterniflora, a dominant vascular marsh plant, benefits growth of P. aztecus (Hunter and Feller 1987; Gleason and Wellington 1988). Vascular

plant fragments, however, have been observed in the digestive system of the shrimp (Williams 1955; Jones 1973). While Spartina detritus is a potential food source, its value appears questionable, because it does not produce growth in the animals (Gleason and Zimmerman 1984). While *P. aztecus* may consume detrital material, it evidently is poorly assimilated (Jones 1973). Brown shrimp survived when fed plant-based diets, but their rate of growth was at maintenance levels (Zein-Eldin 1963; Gleason and Zimmerman 1984).

The diet of *P. setiferus* has been less studied than that of *P. aztecus*. The white shrimp is also identified as an omnivore (Weymouth et al. 1933; Broad 1965) and was previously thought to be a more selective feeder than brown shrimp (Karim 1970; Lindner and Cook 1970). Animal protein is consumed and supports growth in *P. setiferus* (Hunter and Feller 1987; McTigue and Zimmerman 1991). The gut contents of juvenile white shrimp usually contain unrecognizable matter, but remains of polychaetes, tanaids, copepods, forams, ostracods, and fish have been positively identified (Williams 1955; Mayer 1985). As the shrimp grow, they seem to select larger prey items (Mayer 1985). Immunological analysis, though, showed that the breadth of dietary selection does not change as the juveniles age (Hunter and Feller 1987). During their postlarval development, these shrimp show a substantial increase in the production of amylase (Lovett and Felder 1990). This may correlate to dietary changes over time, but the interpretation is not yet clear. The penaeid's gut

fullness seems to peak at dawn and remain relatively consistent at other times, regardless of the tidal stage (McTigue and Feller 1989). P. setiferus appears to feed more actively at night than during the day (Mayer 1985). This may be an adaptation to avoid predation by visual feeders.

Spartina alterniflora was not detected by immunological methods in the digestive system of the white shrimp (Hunter and Feller 1987), although unidentified vascular plant material has been observed in gut content material (Williams 1955; Jones 1973). Many plant-based diets produce little or no growth in this species, but white shrimp postlarvae fed the diatom Skeletonema grew at a rate, up to day 20 of the experiment, that was not significantly different from growth resulting from an animal based diet. By day 24, though, the Skeletonema fed shrimp all died, while the animal diet group survived (McTigue and Zimmerman 1991). Penaeus setiferus has been shown to feed on plants in nature and the intensity of that feeding varies on a daily basis (Hunter 1984). Detritus is also a potential food source for the white shrimp (Darnell 1961). However, in laboratory studies, white shrimp fed natural detritus did not grow and died more quickly than shrimp in other treatment groups, including those starved (McTigue and Zimmerman 1991).

Both Penaeus aztecus and Penaeus setiferus demonstrated increased growth when fed combination animal and plant diets over animal or plant diets alone (McTigue and Zimmerman 1991). There is evidence suggesting a difference in the extent to which

the two species utilize potential plant and animal resources. Brown shrimp grow significantly more in length and weight when fed an animal diet than do the white shrimp. The addition of plant material causes both species to grow at increased levels that are not significantly different from one another (McTigue and Zimmerman 1991). The plant material may be of greater significance in the diet of the white shrimp than in that of the brown shrimp. Preliminary research suggests that differences, such as this, in feeding between the shrimp species may be linked to differences in the life cycles of the animals (McTigue and Zimmerman 1991).

While in estuarine areas, the spatial distributional patterns of the two species differ. Brown shrimp are seasonally attracted to the marsh surface, occurring there in higher densities than in open water areas from late March to November. During the winter months, Penaeus aztecus are present in very low numbers and are equally distributed between the marsh surface and the unvegetated, adjacent subtidal bottom. White shrimp are often not significantly different in density between for the marsh surface and subtidal bottom during their residence period (Zimmerman and Minello 1984; Zimmerman et al. 1984; Minello and Zimmerman 1985). These spatial distribution patterns, too, may indicate dietary differences between the species.

If juvenile Penaeus make significant use of infaunal organisms, the structure of the infaunal community may play an important role in the local success of brown shrimp. Infaunal

species can vary in their accessibility to the shrimp and thus affect the amount of food available. There is, however, an important converse question. Do brown shrimp also help to regulate infaunal population levels through predation pressure?

Evidence suggests that interactions occur between demersal organisms and those making up the infauna in soft substrate areas. These interactions are through predation or disturbance, although the results of the two can be difficult to separate (Young *et al.* 1976; Virnstein 1977; Woodin 1978; Young and Young 1978; Arntz 1980; Nelson 1981; Kneib and Stiven 1982; Kent and Day 1983; Leber 1985). The actions of demersal and nektonic organisms can selectively maintain certain infaunal population density levels (Bell and Coull 1978; Kneib and Stiven 1982), as well as determine species composition for an area (Reise 1977; Wooden 1981; Kneib 1985). Stephenson (1980) found a strong relationship between the abundance of Penaeus plebejus, the king prawn, and infauna densities in Moreton Bay, Australia. While there was a strong correlation when considering a zero time lag ($r^2=0.683$), the most significant trend was between infaunal densities and the abundance of shrimp during the previous month ($r^2=0.765$). When shrimp populations increased, infauna decreased. Further these differences may vary significantly among habitats according to the accessibility of the prey and the suite of predators present. As noted previously, infaunal densities in salt marshes and the adjacent open bottom area reach their seasonal peak in late winter or early spring. Their decline

coincides with the arrival of juvenile organisms including brown shrimp and a variety fish (Cammen 1979; Alon and Stancyk 1982; Kneib and Stiven 1982; Coull and Palmer 1984; Kneib 1984; Coull 1985; Flint and Kalke 1985; Zimmerman et al. 1990). What role individual species of immigrants, such as P. aztecus, play in the decline is not yet clear.

A need exists to examine similarities and differences in feeding preferences of Penaeus setiferus and Penaeus aztecus with reference to naturally occurring prey in estuarine systems. Previous studies involving the consumption of animal based diets by shrimp most often have utilized animals such as Artemia, which do not coexist with the shrimp in nature. As my dissertation research, I chose to compare and contrast dietary linkages of brown and white shrimp with the dominant infaunal groups present in Texas salt marshes. The objectives of this project were to determine: (1) if brown and white shrimp can successfully remove infauna from natural sediment, (2) if the penaeids grow when utilizing such resources, and (3) if brown shrimp play a role in the regulation of infaunal populations.

The temporal and spatial separation of brown shrimp and white shrimp may indicate food resource separation as well. A comparison of the feeding habits of the two species of penaeid could help to define the role of these animals in Texas salt marsh communities.

METHODS

Infaunal Removal Experiment

Cores of sediment (10 cm in diameter, 8 cm in depth) without vegetation were collected from the surface of a salt marsh in Galveston Island State Park. They were brought into the laboratory and maintained in a temperature controlled water bath (25° C) with a fixed photoperiod (12h of light). Juvenile shrimp were captured by seine from the same marsh. Each animal was weighed and introduced into a core with approximately 8 cm of aerated seawater above the sediment surface. After 4 days, the animals were removed, weighed, and preserved. The sediment from the core was sieved through 500 micron mesh and the infaunal organisms preserved for later enumeration and identification. Control cores, free of shrimp, were maintained side-by-side with the treatment cores. Both treatment and control groups consisted of at least eight cores of sediment. This procedure was repeated 4 times, twice using brown shrimp (beginning February 23, 1990, and again on May 31, 1990) and twice using white shrimp (beginning on August 10, 1990, and on October 29, 1990). The timing coincided with initial immigration of the species (early season) and the second was near the end of their residence period (late season). Sieved cores that contained potential competitors for the introduced shrimp were discarded. Potential competitors included grass shrimp, fiddler crabs, and

other penaeids. A comparison of the effects on infaunal abundance was made for each shrimp species both early and late during their residence period.

T-tests were used to determine differences between the treatment and control cores, both for overall abundances within major taxonomic groups and for each of the numerically dominant infaunal species. Results of the t-tests were compared, but the data were not pooled.

Growth Experiment

To determine differences in growth response of the two species to naturally available foods, the following categories were chosen: amphipods, polychaetes, the diatom Skeletonema costatum, amphipods plus Skeletonema, and polychaetes plus Skeletonema. These categories were selected based upon high natural abundance in the marsh. In the case of Skeletonema, previous experimentation indicated that this diatom produced more growth in juvenile shrimp than any other algae considered (Gleason and Zimmerman 1984; McTigue and Zimmerman 1991). Species of polychaetes and amphipods were provided in the same relative proportions in which they were collected from the field.

Both species of shrimp were fed material from each of the above categories as treatments and starved controls were maintained. Each treatment and control group consisted of twenty penaeids kept individually. Growth over a period of 30 days was

determined as well as the amount of animal material consumed. The shrimp were held in aerated, filtered seawater (300 ml) in individual 800 ml beakers at 25°C with 12 hours of light per day. Food was provided ad libitum, with both weight and number of prey organisms provided recorded, and the water changed every 5 days. Size ranges of prey were randomly mixed, but groups with all large prey items were disregarded. New prey items were added during the 5 day intervals when the beakers became depleted. The diatom Skeletonema was grown in the laboratory using F2 medium (Guillard 1975). The cultures were centrifuged to separate algal cells from culture media. The Skeletonema was then resuspended in filtered (0.5 µm), natural sea water and provided to the shrimp in beakers with a density of 5×10^5 cells per milliliter. Cell counts were monitored periodically and the beakers were enriched if needed. Every 5 days when the water was changed, the penaeids were weighed and the incremental growth calculated.

The number of days each shrimp survived was analyzed and diets and species of the shrimp were compared using ANOVA. The data were log transformed to take into account heterogeneity of variances between treatments. When significant interactions between diet and shrimp species were indicated, contrasts were used to determine relationships between the factors.

The change in weight over the 5 day intervals used in this procedure were used as a measure of growth rate. Interval weight changes for shrimp consuming amphipods, polychaetes,

amphipods plus Skeletonema, and polychaetes plus Skeletonema up to day 20 were analyzed using a repeated measures analysis of variance. This takes into account the relatedness of growth data from one interval to another. Only data up to day 20 were used to insure adequate sample sizes for the four treatment diets. Significant interactions between the species of shrimp and among diets were analyzed with contrasts to further delineate differences.

Predator Exclusion Study

During February, before the seasonal decline of infauna occurred and penaeid abundances were still low, predator exclusion cages were installed on the marsh surface and in the adjacent unvegetated creeks at Galveston Island State Park. A drop sampler (described in Zimmerman et al. 1984) was randomly placed and the water and nektonic and demersal organisms removed from within. The cage was then placed inside the sampler to insure no epibenthic or nektonic animals were included. The cages consisted of cylinders of hardware cloth (2.5 m in diameter, 1.22 m in height) lined with fiberglass window screen (mesh diameter = 1 mm x 1.5 mm). An open edge of the cylinder was then embedded in sediment until 1 m of cage stood above the sediment-water interface. Four wooden stakes were driven into the substrate around the cage and the cage wall affixed to them for stability.

Six paired sites were used, with one vegetated (marsh surface) and one nonvegetated (open water) cage at each location. All cages were placed within two meters of the marsh-open water interface. An initial core was taken inside (prior to cage construction) and outside each cage to determine baseline values of infaunal biomass. Cores were subsequently taken every two weeks for ten weeks, both inside and outside the cages. Control cores (outside the cages) were taken approximately 2 m away from the cage to avoid sediment disturbed by footsteps. Each core was sieved through a 500 μm screen in the field and the infauna preserved (7% formalin with rose bengal) for later identification and counting. The mesh of the cages was brushed clean each week to prevent the restriction of water circulation through fouling by macroalgae.

The response of the infaunal communities within the cages was compared with that of the surrounding area to determine the effects of the removal of predators. Densities of brown shrimp in the same marsh during the ten week experimental duration were obtained from the benthic ecology research group at the National Marine Fisheries Service in Galveston. This information was used to determine the average density of brown shrimp for each two week sampling period. Optimal consumption rates of polychaetes and amphipods (in the presence of algae) were calculated from experimental procedures given in the previously mentioned growth experiment. Consumption rates for shrimp provided algae as well as the faunal dietary items were used because they may

more closely approximate field conditions versus animal material alone. The two values were used to determine an estimate of removal per unit area of polychaete and amphipod biomass during each two week interval. A Hydrolab Data Sonde located near the cages provided hourly water level measurements, which were translated into the percentage of time for each two week period the marsh surface was accessible to shrimp. These percentages were used to qualify the removal rate estimates to more closely approximate natural conditions. A theoretical line was constructed indicating infaunal abundances over time to estimate the effects of brown shrimp feeding in the absence of other predators.

Calculations were made for each cage, using the mean of initial cores taken for the treatment and control as the first N_{t-1} . The subsequent calculations used the density of the immediately preceding interval as N_{t-1} and the number of infauna lost to predation was calculated for each 14 day period. This was to incorporate changing predator densities over time into the prediction.

A repeated measures ANOVA was employed to determine if there were significant differences in the no predation, normal predation levels, and the theoretical shrimp feeding only lines. Dry weight, taken here to indicate biomass, was analyzed for both polychaetes and amphipods. Repeated measures ANOVA were used because the same cages were sampled each time. When a significant interaction between time and treatment (no predators,

all predators, estimate of shrimp only) was indicated, a standard (not a repeat measures) ANOVA was used to construct appropriate contrasts. The test was changed to allow in depth analysis of the time variable, in a manner not permitted by repeated measures analysis.

RESULTS

Infaunal Removal Experiment

Penaeus aztecus significantly reduced the total number of infaunal organisms in the sediment cores during each run of the experiment (Table 1, Fig. 1). Annelids and crustaceans were removed during both periods, although the effect was less significant late in the season during May (Figs. 2 and 3). Of the most abundant infaunal worms (Table 2), brown shrimp consistently removed Melinna maculata, Streblospio benedicti, and oligochaetes. Ampelisca abdita, Corophium louisianum, and Hargeria rapax among the crustaceans were reduced early during February when their densities were high, but no crustacean was significantly reduced during May when the potential prey's densities were low. Insects, primarily chironomid larvae (Tables 1 and 2, Figs. 2 and 3), were reduced in February but they did not occur in significant densities in May.

Neither during August nor October did white shrimp significantly reduce numbers of any taxonomic category of infauna considered in core feeding experiments (Tables 3 and 4, Figs. 4 and 5). None of the most abundant species of annelids or crustaceans were reduced in abundance by Penaeus setiferus.

A comparison of growth over the four day period of exposure to the sediment cores showed that white shrimp grew

consistently less than did the brown shrimp (Fig. 6). This was evident in both early and late trials of the study.

Table 1. Results of t-tests comparing infaunal organismal abundances between control cores of sediment and those in which brown shrimp had fed for four days. Taxa marked with an asterix had unequal variances and were treated accordingly.

February 23,1990

Taxon	T	d.f.	p-value
total	4.3009	14	0.0007
annelids	3.1957	14	0.0065
crustaceans*	3.3827	9.4	0.0077
insects	3.0656	14	0.0084

May 31,1990

Taxon	T	d.f.	p-value
total*	2.3697	11	0.0373
annelids*	2.2666	11.7	0.0432
crustaceans*	2.349	9.5	0.0421
insects*	0.9694	21	0.2924

Table 2. Results of t-tests comparing control cores to those in which brown shrimp fed for four days. Abundances are of individual species of infaunal organisms. An asterix indicates that the variances were unequal and handled accordingly.

February 23,1990

Annelids	T	d.f.	p-value
<u>Capitella capitata</u>	1.4491	14	0.1693
<u>Heteromastus filiformis</u>	1.7052	14	0.1102
<u>Leitoscoloplos fragilis</u>	1.6667	14	0.1178
<u>Melinna maculata</u>	2.3593	14	0.0334
<u>Streblospio benedicti</u>	2.827	14	0.0134
oligochaetes*	3.0314	8.8	0.0146
Crustaceans			
<u>Ampelisca abdita*</u>	2.6848	7.7	0.0289
<u>Corophium louisianum</u>	2.47	14	0.027
<u>Edotea sp.*</u>	-1.727	8.6	0.1199
<u>Grandiderella bonneroides*</u>	1.0435	7.9	0.3277
<u>Hargeria rapax*</u>	2.4873	7.7	0.0388
Insects			
chironomid larvae	3.2062	14	0.0063

May 31,1990

Annelids	T	d.f.	p-value
<u>Capitella capitata</u>	-0.2185	21	0.8292
<u>Melinna maculata*</u>	-1.7942	14.9	0.0931
<u>Streblospio benedicti</u>	2.6945	21	0.0136
oligochaetes*	1.2362	9.1	0.3082
Crustaceans			
<u>Ampelisca abdita</u>	1.2016	21	0.2429
<u>Corophium louisianum*</u>	1.462	11	0.1717
<u>Hargeria rapax*</u>	1.7518	9.1	0.1133
harpacticoid copepods	1.4019	9.1	0.1942

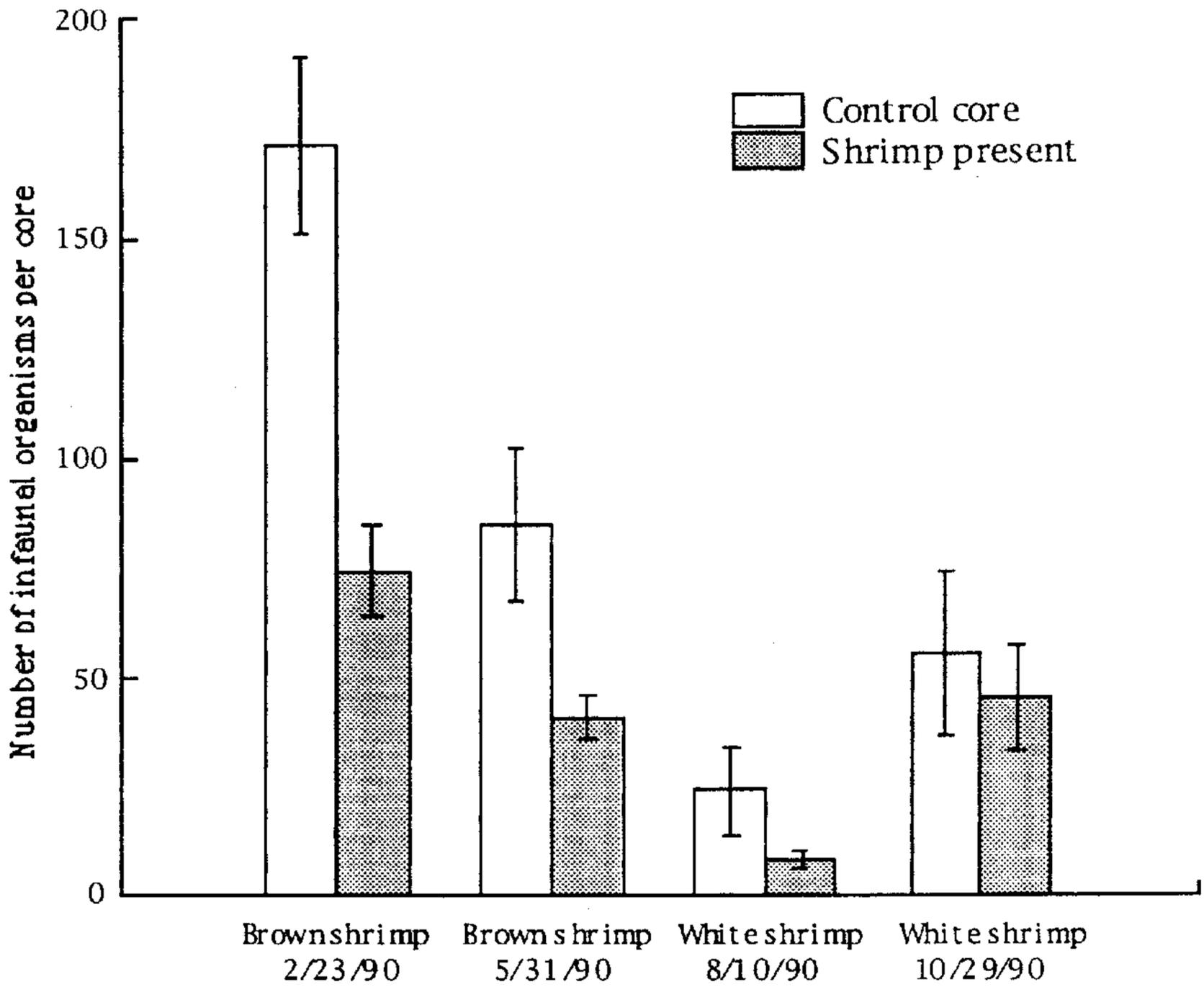


Figure 1. A comparison of infaunal densities between control cores and cores in which penaeid shrimp have fed for four days. The species of shrimp and date of initiation of the experiment are noted below the bars. Error bars indicate one standard error. Each core had a surface area of 78.54 cm² and a depth of 8 cm.

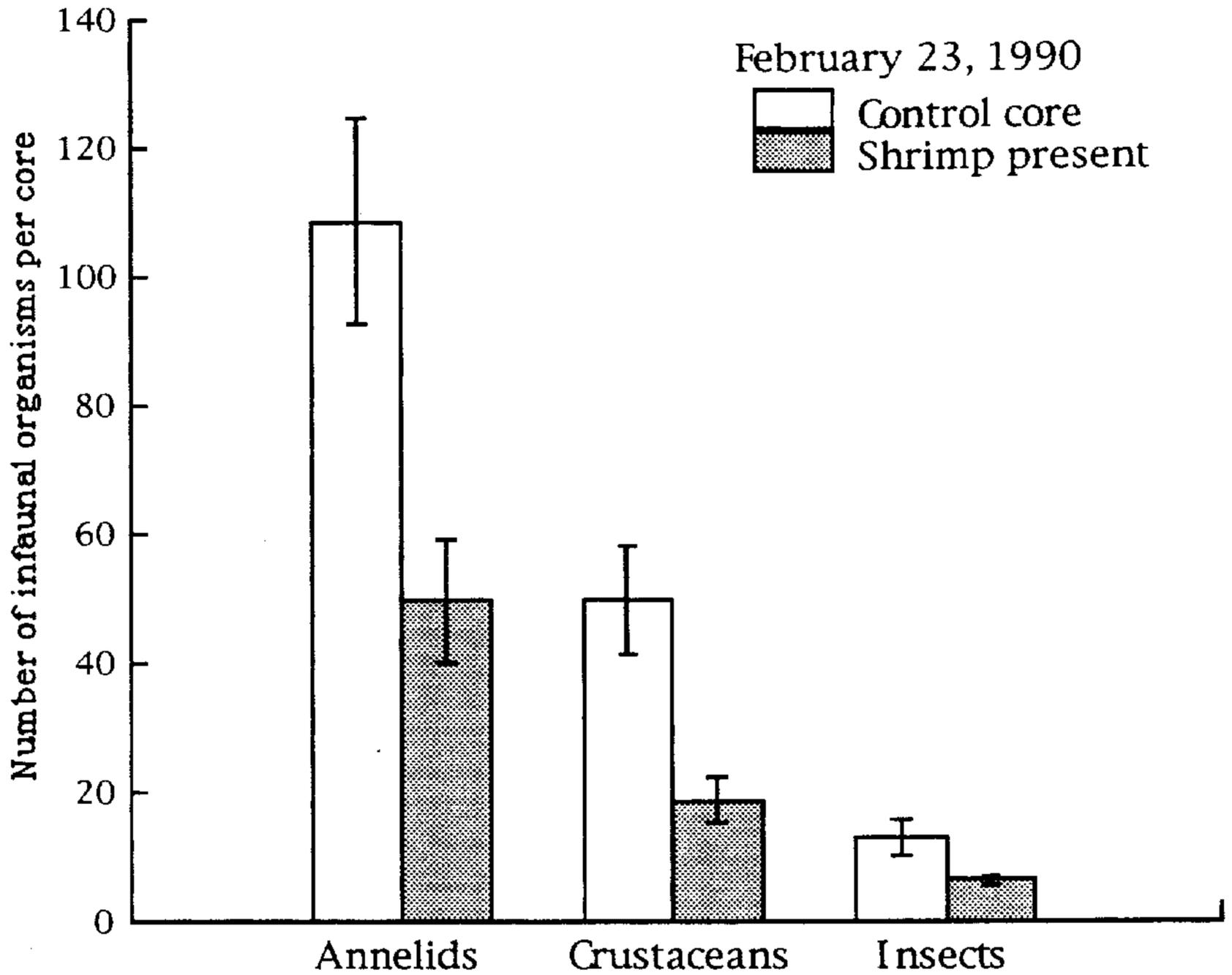


Figure 2. Depletion of infauna in cores (78.54 cm^2) in which brown shrimp were held for four days beginning February 23, 1990. Error bars indicate one standard error.

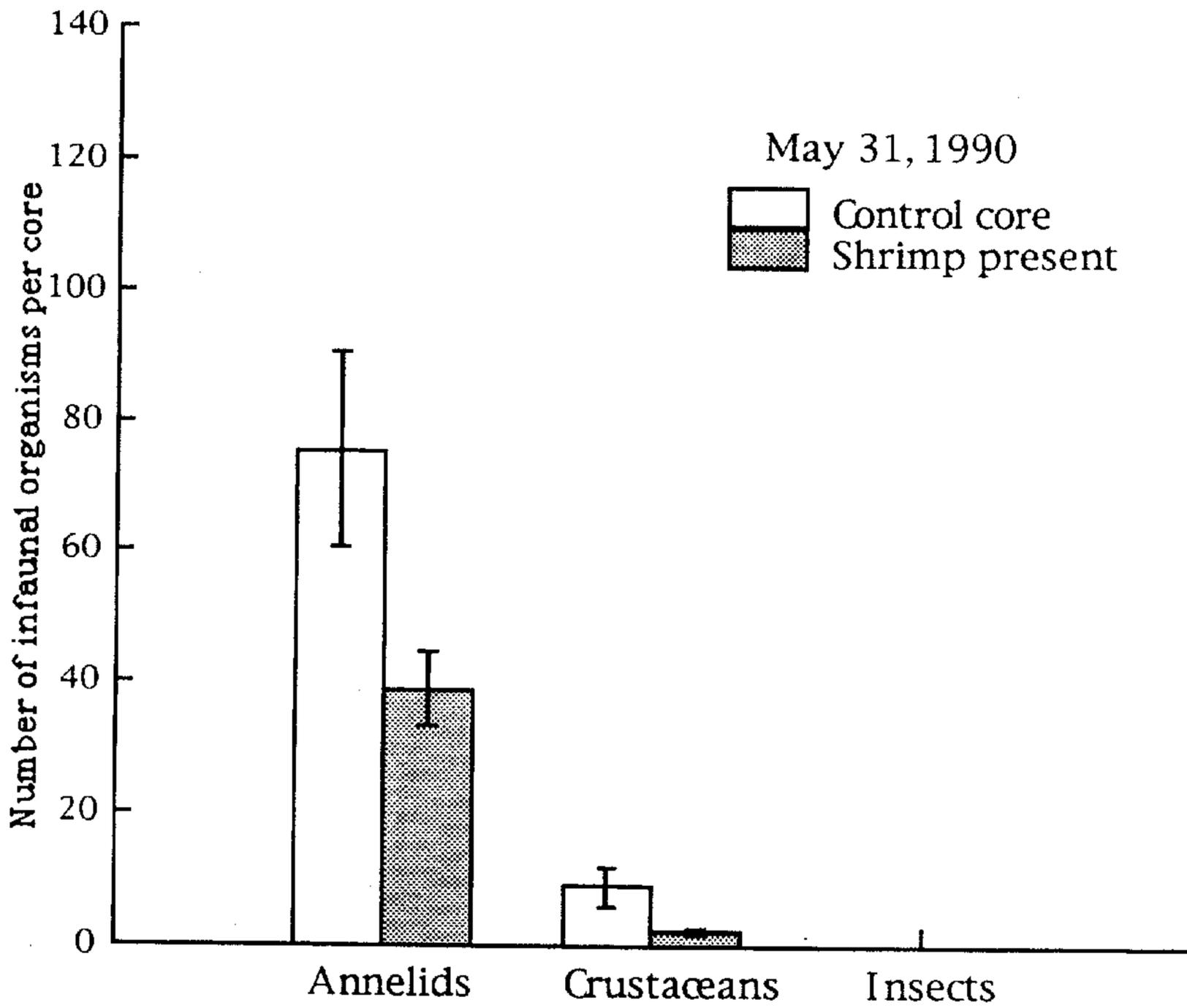


Figure 3. Depletion of infauna in cores (78.54 cm^2) with brown shrimp over four days beginning May 31, 1990. Error bars indicate one standard error.

Table 3. Results of t-tests comparing infaunal organismal abundances between control cores of sediment and those in which white shrimp had fed for four days. Taxa marked with an asterix had unequal variances and were treated accordingly.

August 10, 1990

Taxon	T	d.f.	p-value
total*	1.524	10	0.1585
annelids*	1.9737	5.4	0.102
crustaceans	-0.3492	10	0.7342

October 29, 1990

Taxon	T	d.f.	p-value
total	0.4333	10	0.674
annelids	0.4397	10	0.6695
crustaceans	-0.2863	10	0.7805

Table 4. Results of t-tests comparing control cores to those in which white shrimp fed for four days. Abundances are of individual species of infaunal organisms. An asterix indicates that the variances were unequal and handled accordingly.

August 10,1990

Annelids	T	d.f.	p-value
<u>Capitella capitata</u> *	1.1763	5.3	0.2902
<u>Neanthes succinea</u> *	1.1169	5.1	0.314
<u>Streblospio benedicti</u> *	1.5624	5.3	0.1757
Crustaceans			
<u>Corophium louisianum</u>	-0.0991	10	0.923

October 29,1990

Annelids	T	d.f.	p-value
<u>Capitella capitata</u>	0.8497	10	0.4154
<u>Neanthes succinea</u>	0.3147	10	0.7595
<u>Streblospio benedicti</u>	0.0978	10	0.924
oligochaetes*	1.6606	6.2	0.1461

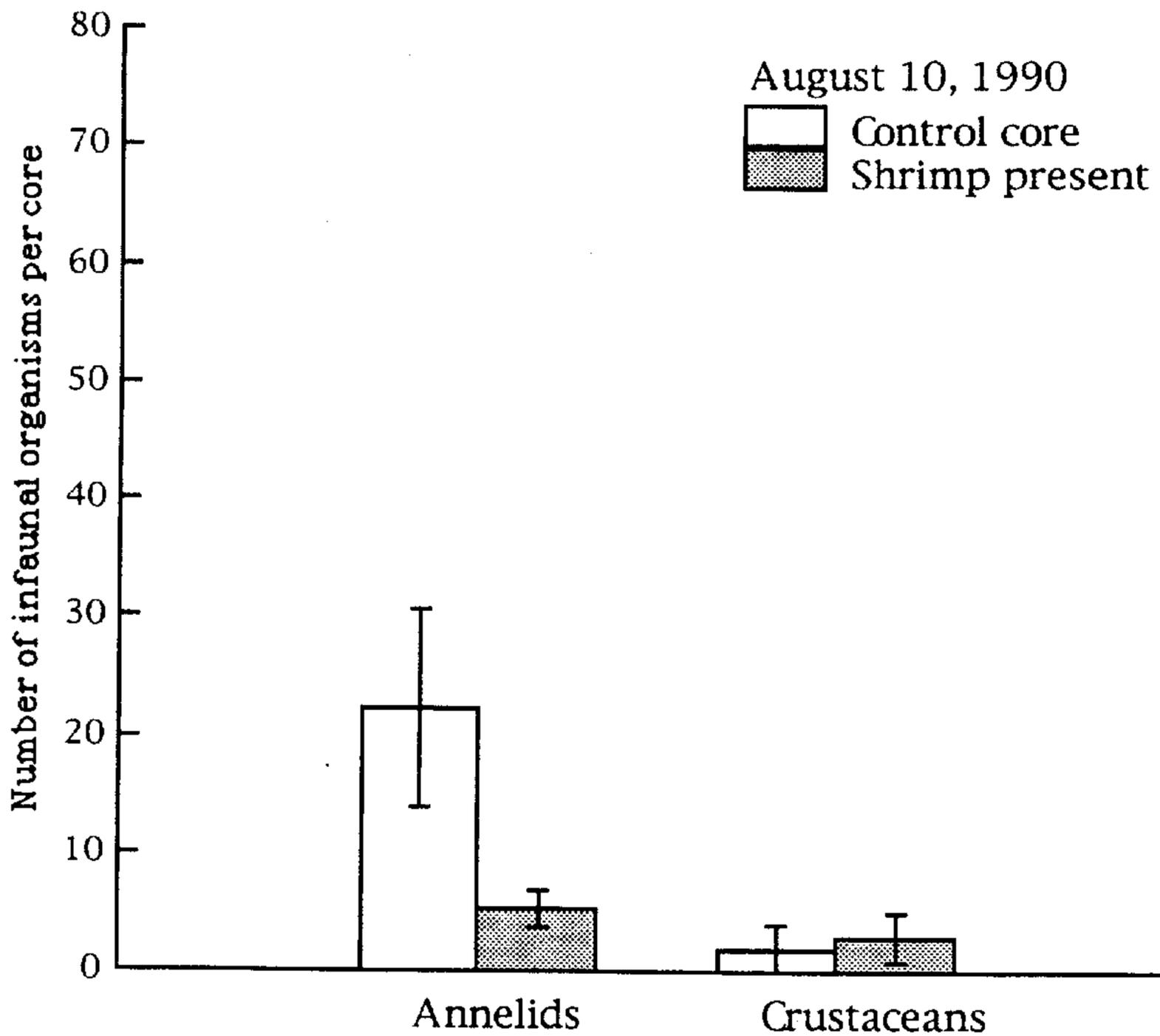


Figure 4. Depletion of infauna from cores of sediment (area = 78.54 cm²) in which white shrimp were placed for four days beginning August 10, 1990. Error bars indicate one standard error.

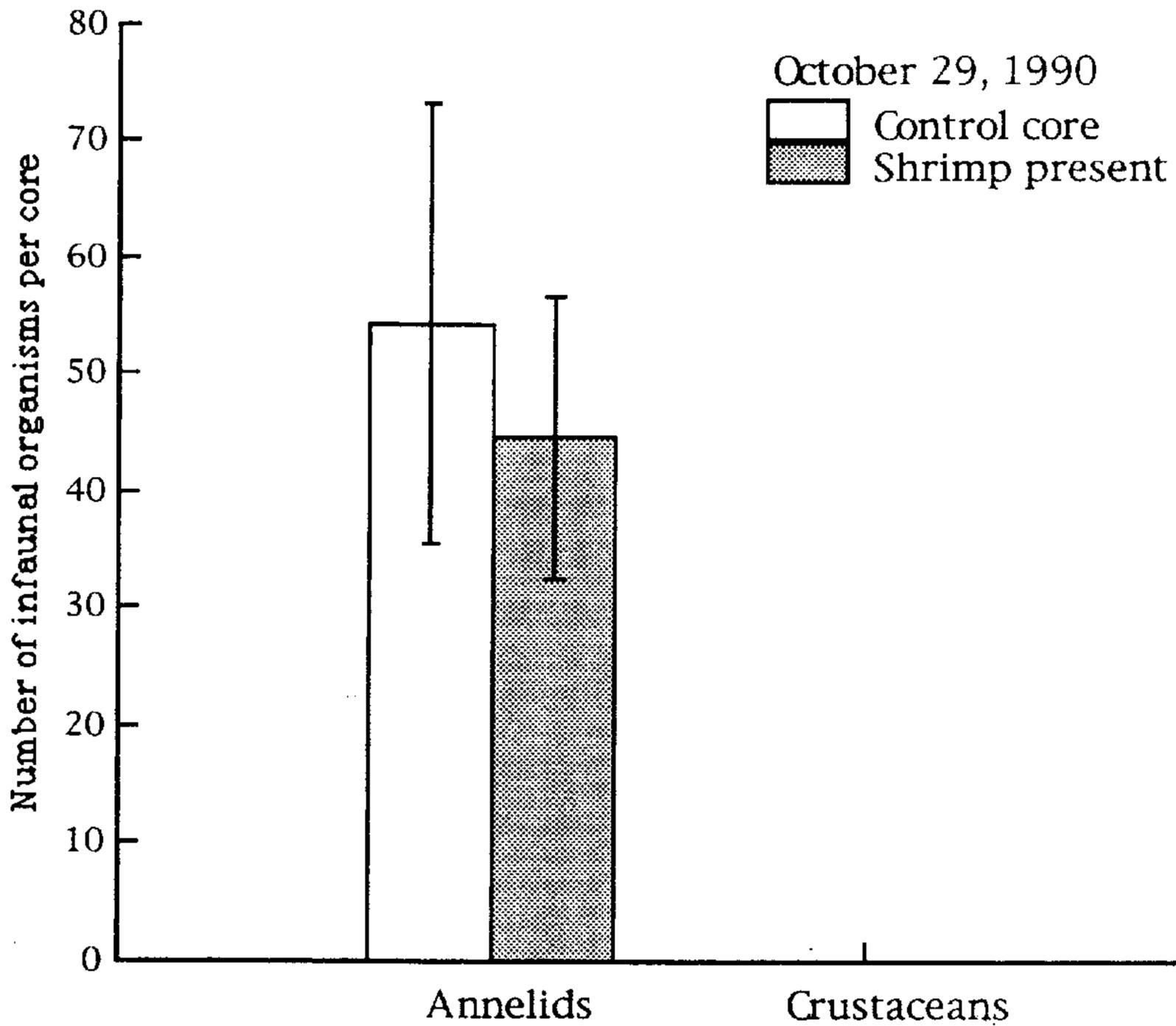


Figure 5. Depletion of infauna from cores (area = 78.54 cm²) in which white shrimp were held for four days beginning October 29, 1990. Error bars indicate one standard error.

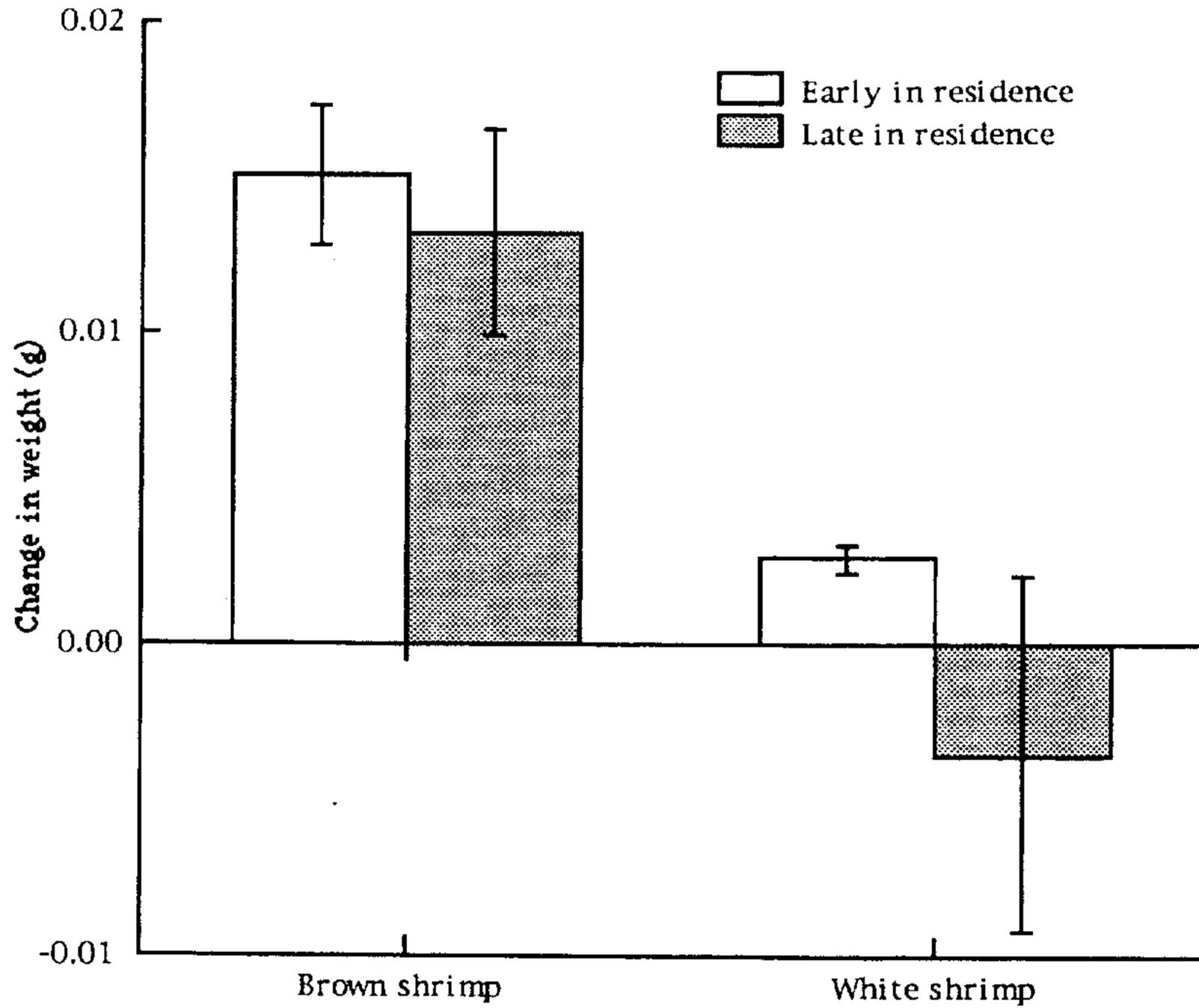


Figure 6. Weight change for brown and white shrimp during a four day exposure to cores of natural sediment. Experimental runs occurred early and late during the residence period of each shrimp species. Error bars indicate one standard error.

Growth Experiment

During the thirty day growth experiments, there were significant differences between survival of Penaeus aztecus and Penaeus setiferus fed similar diets (Tables 5 and 6, Fig. 7). While survival of both species was similar when the experimental diets included polychaetes, overall, brown shrimp lived longer. White shrimp survival was significantly reduced in amphipod based treatments as compared to the brown shrimp. Similarly, when plant-animal combination diets or animal material only diets were considered, white shrimp survived in lower numbers than did the brown shrimp.

The addition of animal material to a diet increased the survival in both species compared to Skeletonema alone (Tables 7 and 8). Conversely, the addition of algae did not significantly affect the survival of brown shrimp, regardless of the animal material offered. White shrimp did not show a difference in survival between the amphipod and amphipod + Skeletonema treatments, although they lived longer on a polychaete diet versus polychaetes + Skeletonema. White shrimp were able to survive longer on polychaete based and combination plant-animal diets than on all others. Brown shrimp showed no difference in growth between polychaete based diets, although combination diets prolonged survival.

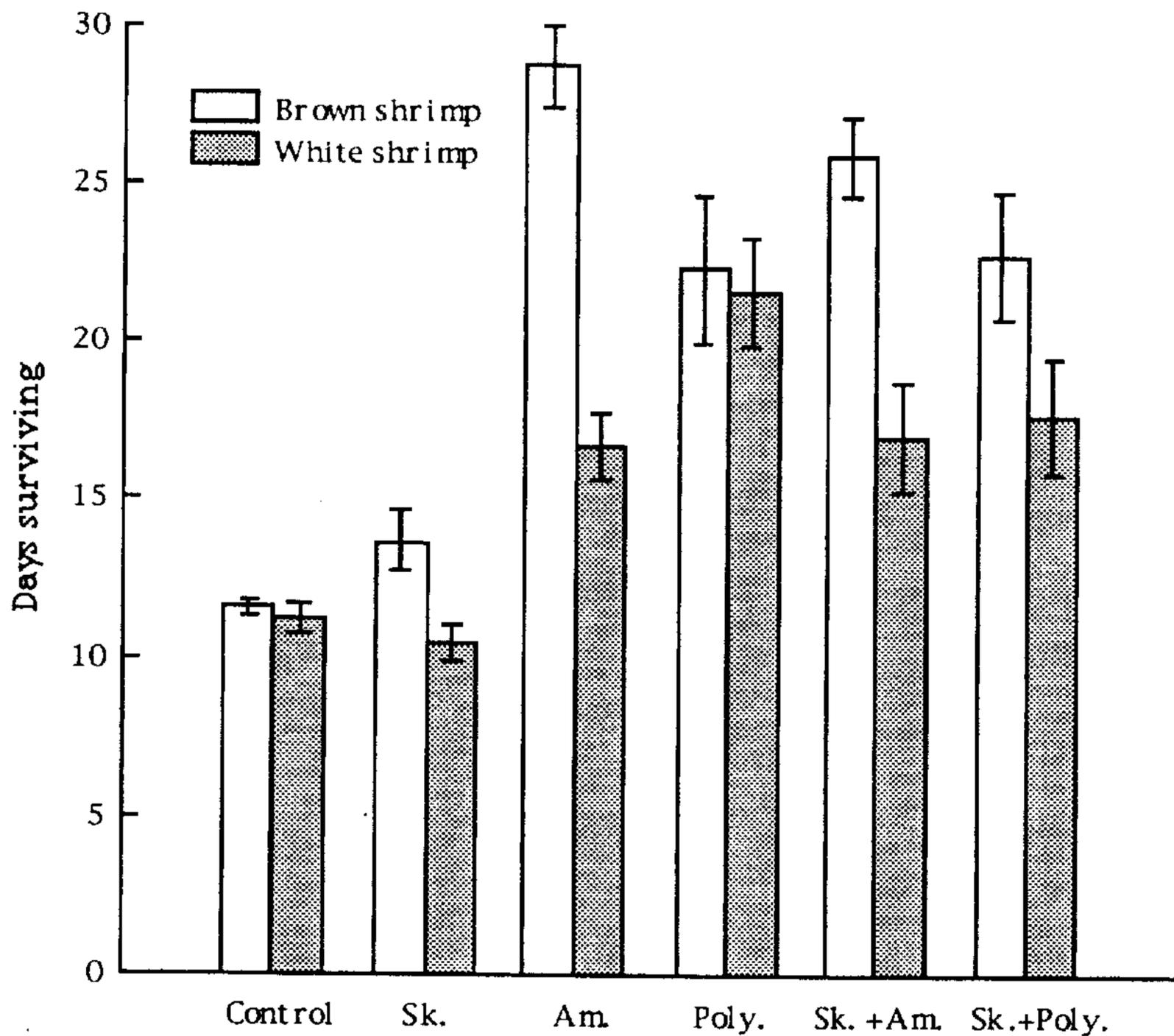


Figure 7. Number of days brown and white shrimp survived in experimental containers when fed the following treatment diets: Control = starved, Sk. = Skeletonema, Am. = amphipods, Poly. = polychaetes, Sk. + Am. = Skeletonema and amphipods, Sk. + poly. = Skeletonema and polychaetes. Error bars indicate one standard error.

Table 5. Analysis of variance of survival of brown and white shrimp fed experimental diets. Data were log transformed because of heterogeneity of variances.

Dependent variable:

days survived (log transformed)

Source	d.f.	Sum of Squares	Mean Square	F Value	P Value
model	11	26.894414	2.444947	20.18	0.0001
error	268	32.464481	0.121136		
corrected total	279	59.358895			

Source	d.f.	Type III S.S.	Mean Square	F Value	P Value
species	1	4.268249	4.268248	35.24	0.0001
diet	5	21.561981	4.312396	35.6	0.0001
species* diet	5	2.751237	0.550247	4.54	0.0005

Table 6. Contrasts performed on shrimp survival data within and between species of shrimp. The numbers refer to the p-value of the contrast and an asterix denotes significant differences at the alpha = 0.05 level.

Contrast	F Value	P Value
Brown vs. white overall	35.24	*0.0001
Brown vs. white animal+plant diets	16.94	*0.0001
Brown vs. white animal material only diets	14.96	*0.0001
Brown vs. white polychaete based diets	2.42	0.1211
Brown vs. white amphipod based diets	42.13	*0.0001

Table 7. ANOVA contrast procedure performed on shrimp survival data for brown shrimp. The numbers refer to the p-value of the contrast and an asterix denotes significant differences at the alpha = 0.05 level.

Contrast	F Value	P Value
polychaete based diets vs. all others	2.5	0.115
control (starved) vs. all others	78.57	*0.0001
combination animal/plant diets vs. all others	17.39	*0.0001
polychaete vs. polychaetes + Skeletonema	0.14	0.7073
amphipod vs. amphipod + Skeletonema	0.78	0.3776
Skeletonema vs. combination animal/plant	29.38	*0.0001

Table 8. ANOVA contrast procedures performed on shrimp survival data for white shrimp. The numbers refer to the p-value of the contrast and an asterix denotes significant differences at the $\alpha = 0.05$ level.

Contrast	F Value	P Value
polychaete based diets vs. all others	22.02	*0.0001
control (starved) vs. all others	34.46	*0.0001
combination animal/plant diets vs. all others	5.65	*0.0182
polychaete vs. polychaetes + Skeletonema	15.78	*0.0001
amphipod vs. amphipod + Skeletonema	0.02	0.8969
Skeletonema vs. combination animal/plant	14.78	*0.0002

When incremental growth was considered, species*diet and time*diet interactions were significant for the overall model (Table 9). Within each 5 day increment of time, the species*diet interaction was consistently significant (Table 10).

Table 9. Repeated measures analysis of variance (ANOVA) of incremental growth of brown and white shrimp fed experiment diets. Data were log transformed because of heterogeneity of variances. The analysis included 20 days of the growth study. An asterix indicates significance at the $\alpha = 0.05$ level.

Dependent variable: weight change in 5 days (log transformed)

Tests of hypotheses for between subject effects

Source	d.f.	Type III S.S.	Mean Square	F Value	P Value
species	1	0.0193797	0.0193797	192.29	*0.0001
diet	3	0.0379416	0.0126472	125.49	*0.0001
species*diet	3	0.0184337	0.00614456	60.97	*0.0001
error	73	0.00735371	0.0001008		

Tests of hypotheses for within subject effects

Source	d.f.	Type III S.S.	Mean Square	F Value	P Value
time	3	0.003994	0.001331	6.94	*0.0002
time*species	3	0.000017	0.000006	0.03	0.9934
time*diet	9	0.004687	0.000521	2.71	*0.0051
time*species*diet	9	0.002306	0.000256	1.34	0.2198
error	219	0.042011	0.000192		

Table 10. Repeated measures analysis of variance (ANOVA) of incremental growth of brown and white shrimp fed experiment diets. Data were log transformed because of heterogeneity of variances. The analysis included 20 days of the growth study. An asterix indicates significance at the $\alpha = 0.05$ level.

Dependent variable: weight change in 5 days (log transformed)

Initial to day 5 F Value = 13.68 P Value = 0.0001*

Source	d.f.	Type III S.S.	Mean Square	F Value	P Value
species	1	0.004701	0.0047001	26.68	*0.0001
diet	3	0.005424	0.001808	10.26	*0.0001
species*diet	3	0.004549	0.001516	8.61	*0.0001

Day 5 to day 10 F Value = 34.17 P Value = 0.0001*

Source	d.f.	Type III S.S.	Mean Square	F Value	P Value
species	1	0.005261	0.005261	66.62	*0.0001
diet	3	0.008903	0.002968	37.58	*0.0001
species*diet	3	0.00364	0.001213	15.36	*0.0001

Day 10 to day 15 F Value = 13.39 P Value = 0.0001*

Source	d.f.	Type III S.S.	Mean Square	F Value	P Value
species	1	0.004497	0.004498	23.39	*0.0001
diet	3	0.008824	0.002941	15.3	*0.0001
species*diet	3	0.002562	0.000854	4.44	*0.0064

Day 15 to day 20 F Value = 26.84 P Value = 0.0001*

Source	d.f.	Type III S.S.	Mean Square	F Value	P Value
species	1	0.004937	0.004937	21.58	*0.0001
diet	3	0.019478	0.006493	28.37	*0.0001
species*diet	3	0.009988	0.003329	14.55	*0.0001

When contrasts were constructed using the species*diet interaction term for the entire model, patterns became evident both between and within species. Brown shrimp consistently grew more quickly than white shrimp (Table 11, Figs. 8 and 9).

Table 11. Contrasts associated with ANOVA procedures performed on shrimp incremental growth data within and between species of shrimp including polychaete, amphipod, polychaete + Skeletonema, and amphipod + Skeletonema diets. The numbers refer to the p-value of the contrast and an asterix denotes significant differences at the alpha = 0.05 level.

Contrast	Period of time			
	Initial- Day 5	Days 5- 10	Days 10-15	Days 15-20
Brown vs. white overall	*0.0001	*0.0001	*0.0001	*0.0001
Brown vs. white animal+plant diets	0.0987	*0.0001	*0.0115	0.0548
Brown vs. white polychaete based diets	*0.0001	*0.0001	*0.0001	*0.0001
Brown vs. white amphipod based diets	0.4164	*0.0460	0.2823	0.4925
Brown vs. white animal material only diets	*0.0001	*0.0001	*0.0001	*0.0001

Further, the brown shrimp maintained a consistently greater weight change than did white shrimp when both were fed polychaete based diets or those consisting of animal material alone. Comparative growth patterns resulting from amphipod-based diets and those containing both plant and animal material were not constant. During some intervals significant differences were evident, while in others there were not differences.

In contrasts considering brown shrimp alone, it is evident that the addition of algae to animal food did not consistently increase the growth rate of the animals (Table 12, Fig. 10). Polychaetes, though, were unvaryingly capable of producing increased growth rates as compared to amphipods. This remained true regardless of the presence of diatoms.

White shrimp did not show any differences between growth resulting from polychaete and polychaete + Skeletonema diets (Table 13, Fig. 11) nor was there a significant difference between the animal-plant combination diets. Shrimp fed amphipods did not consistently differ in their growth rate from either amphipod + Skeletonema or polychaete treatments. The amount of both polychaetes and amphipods consumed over a five day period was calculated for shrimp in the combination animal-vegetal treatments (Fig. 12). Brown shrimp ate more wet weight of polychaetes and amphipods per time interval than did the white shrimp. Neither species consumed as much mass of amphipods as they did of polychaetes.

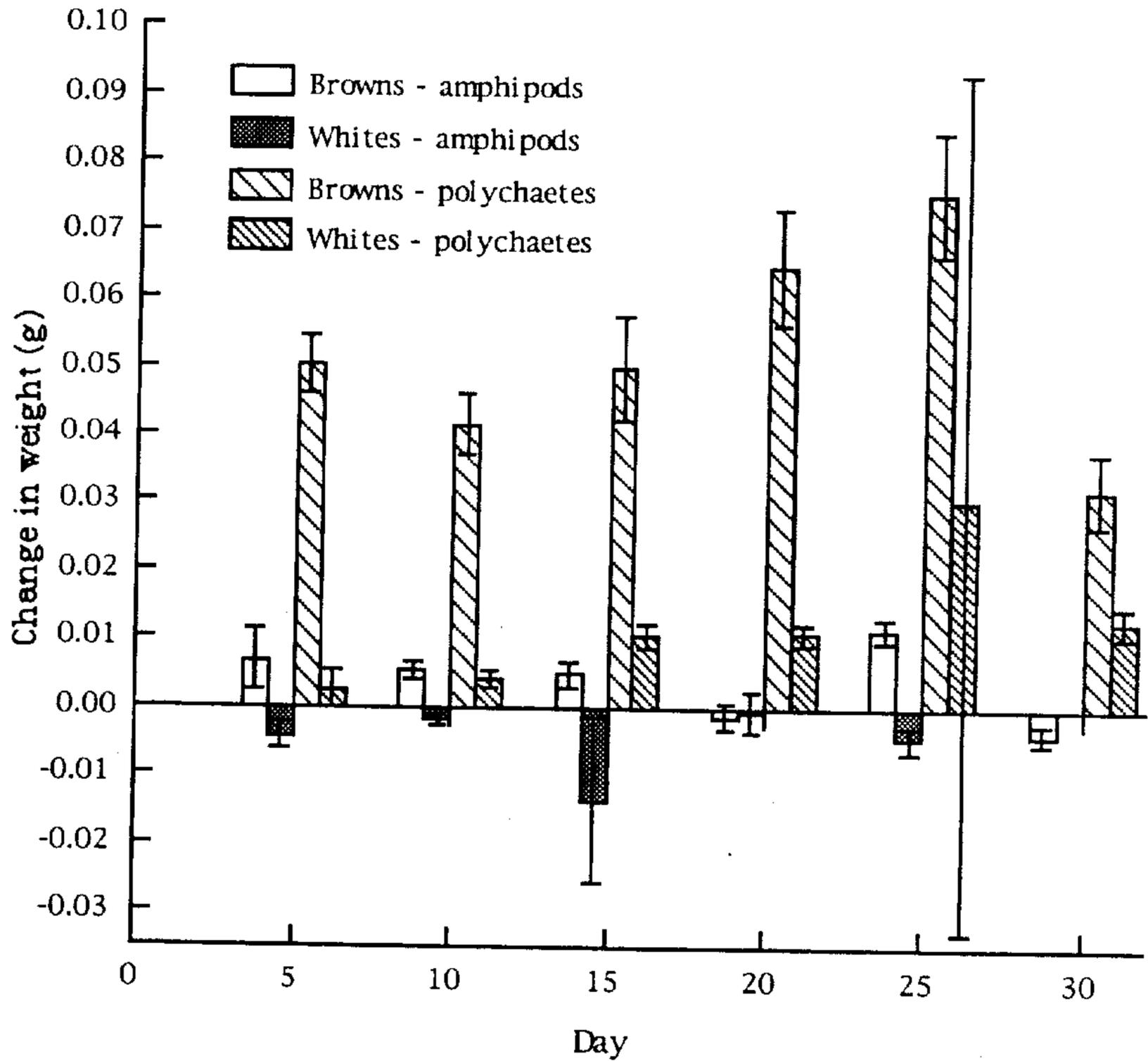


Figure 8. Change in weight for brown shrimp and white shrimp fed amphipod and polychaete diets during 5 day periods over 30 days. Error bars indicate one standard error.

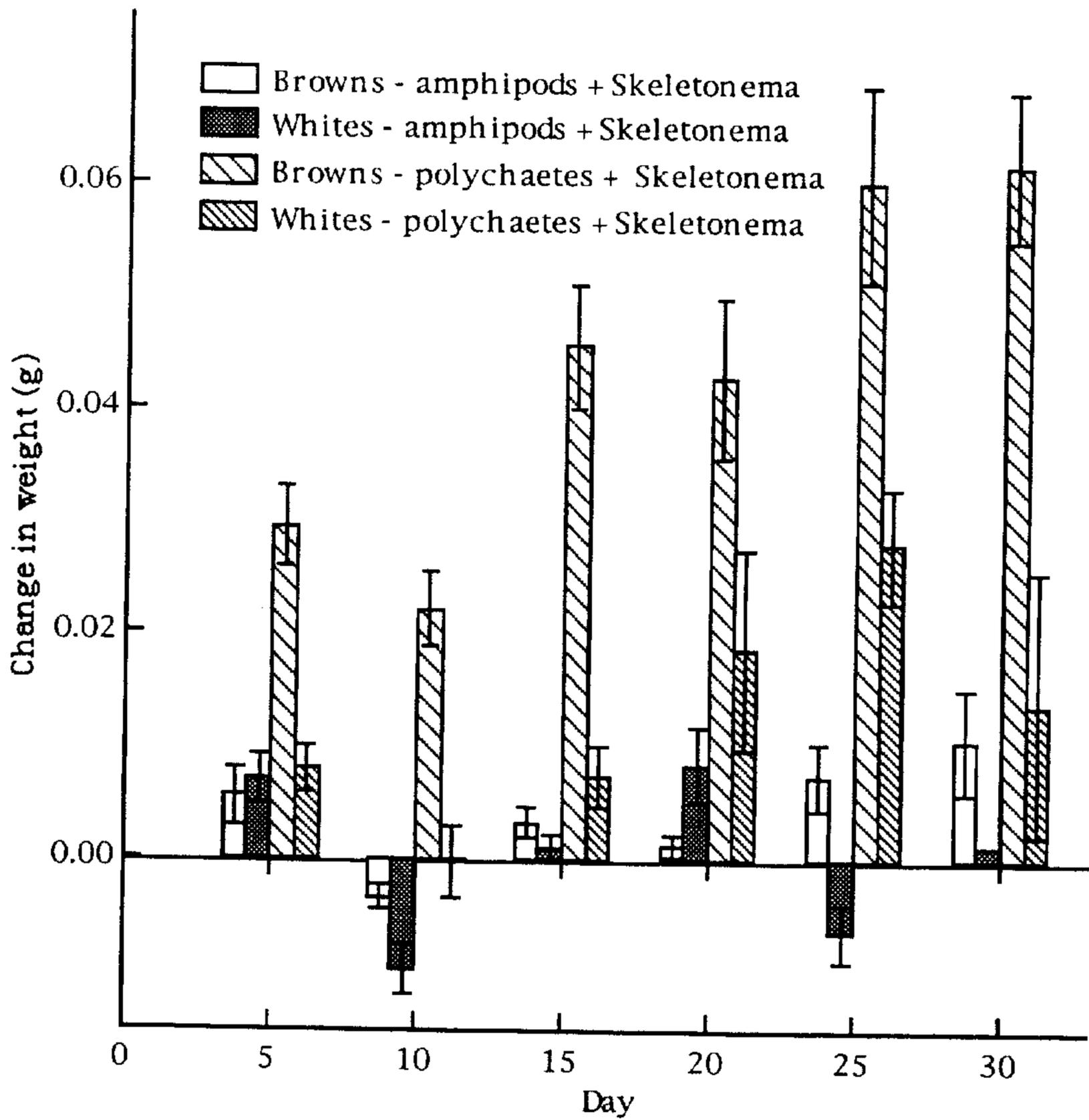


Figure 9. A comparison of weight change for brown shrimp and white shrimp fed combination diets during 5 day periods over 30 days. Error bars indicate one standard error.

Table 12. Contrasts performed during ANOVA procedures on brown shrimp incremental growth data including polychaete, amphipod, polychaete + Skeletonema, and amphipod + Skeletonema diets. The numbers refer to the p-value of the contrast and an asterix denotes significant differences at the $\alpha = 0.05$ level.

Contrast	Period of time			
	Initial- Day 5	Days 5- 10	Days 10-15	Days 15-20
polychaete vs. polychaete + Skeletonema	*0.0444	*0.0001	0.2343	0.1513
amphipod vs. amphipod + Skeletonema	0.3785	*0.0066	0.9252	0.6513
amphipod vs. polychaete	*0.0001	*0.0001	*0.0001	*0.0001
amphipod + Skeletonema vs. polychaete + Skeletonema	*0.0001	*0.0001	*0.0001	*0.0001

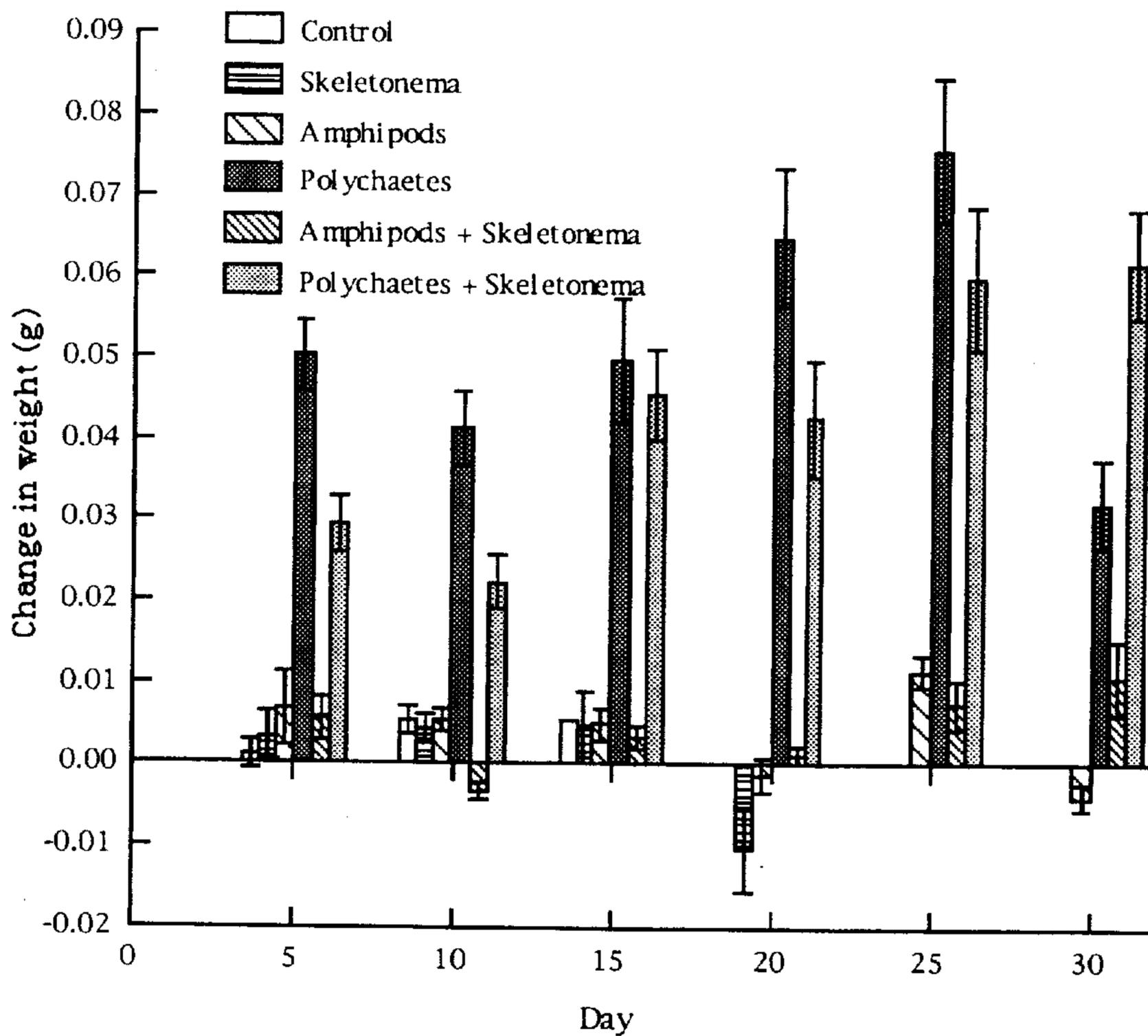


Figure 10. Change in weight over 5 day periods for brown shrimp fed experimental diets of salt marsh infaunal organisms and the diatom *Skeletonema*. Error bars indicate one standard error.

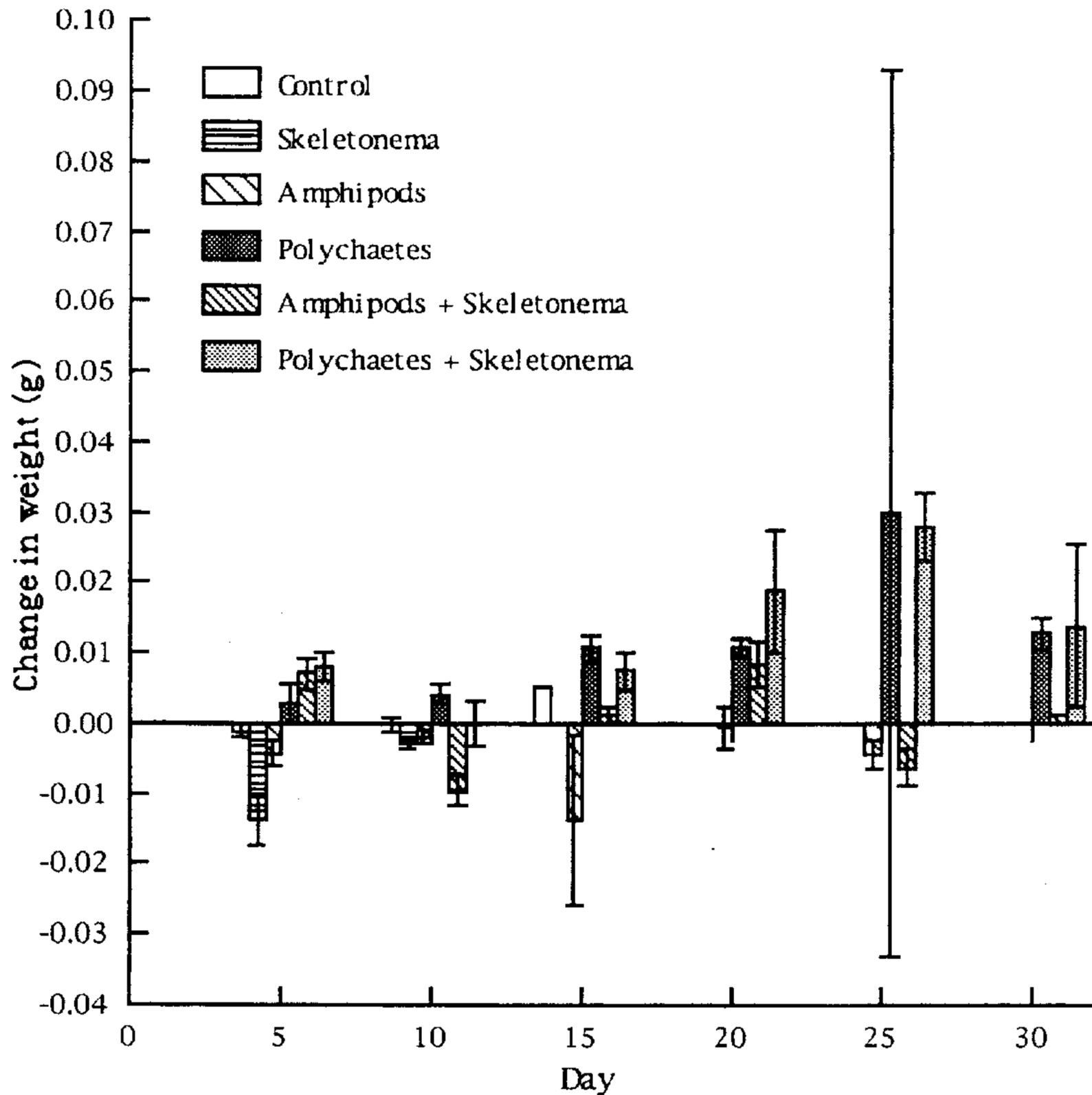


Figure 11. Change in weight over 5 day periods for white shrimp fed experimental diets of salt marsh infaunal organisms. Error bars indicate one standard error.

Table 13. Contrasts performed during ANOVA procedures on white shrimp incremental growth including polychaete, amphipod, polychaete + Skeletonema, and amphipod + Skeletonema diets. The numbers refer to the p-value of the contrast and an asterix denotes significant differences at the $\alpha = 0.05$ level.

Contrast	Period of time			
	Initial-Day 5	Days 5- 10	Days 10-15	Days 15-20
polychaete vs. polychaete + Skeletonema	0.8527	0.4409	0.6277	0.4471
amphipod vs. amphipod + Skeletonema	*0.0220	*0.0189	0.5364	0.3425
amphipod vs. polychaete	0.069	0.5477	*0.0292	0.0832
amphipod + Skeletonema vs. polychaete + Skeletonema	0.3265	0.0951	0.6909	0.3843

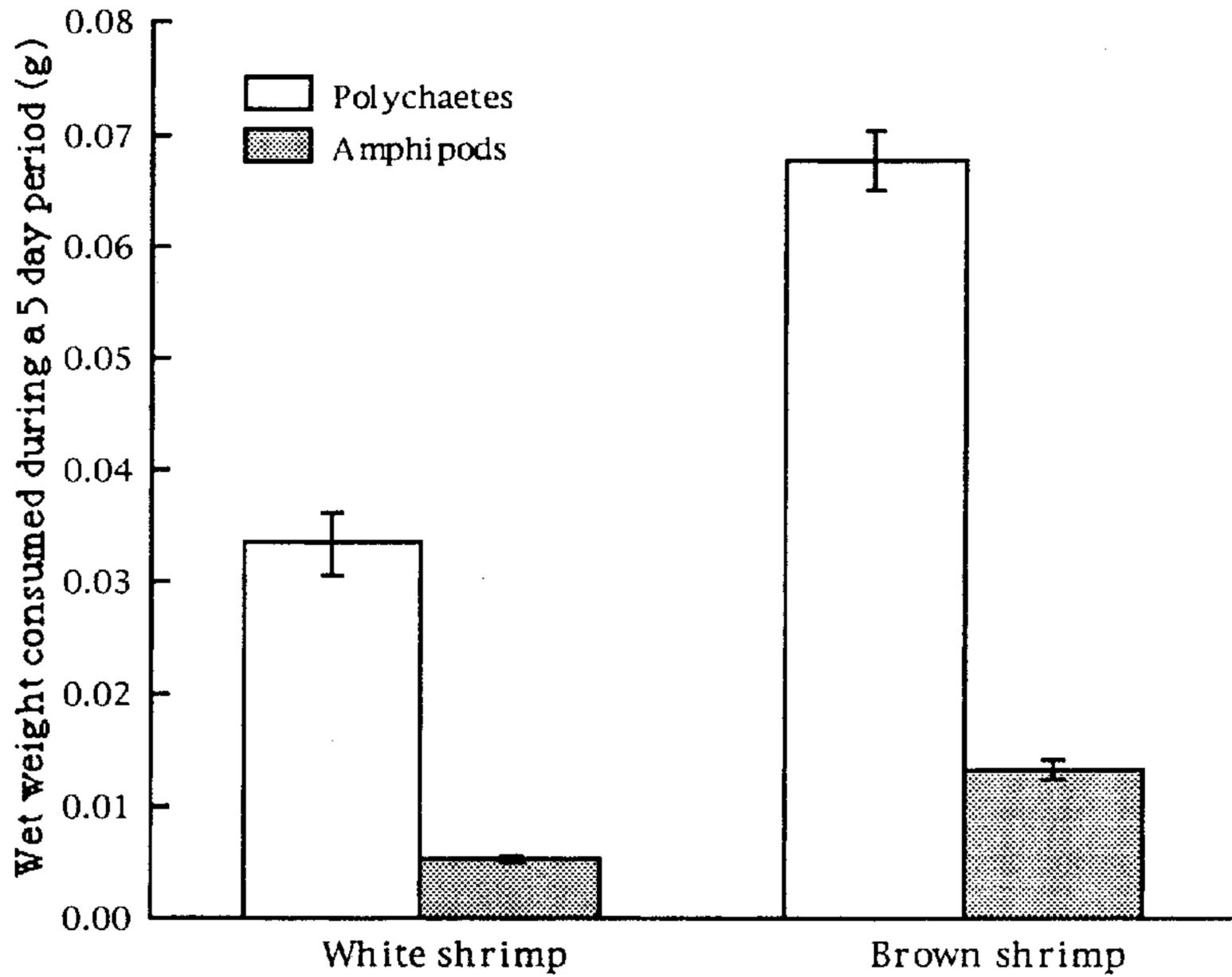


Figure 12. Average consumption of prey items by white and brown shrimp over a five day period. Values are wet weights and are from dietary treatments that included the diatom Skeletonema. Error bars indicate one standard error.

Predator Exclusion Study

Natural densities of brown shrimp and consumption rates determined in the laboratory were used to calculate removal of infauna per unit area (Tables 14 and 15). These values in turn were used to estimate the effects of shrimp feeding alone on infaunal populations (Table 16). There was no significant difference in the change in polychaete biomass among the three treatments over time in vegetated areas (Table 17). Graphic comparison (Fig. 13), however, indicated that at all but two dates (day 42 and 56) the predicted shrimp feeding line was not significantly different from natural predation levels. During the two anomalous dates, large amounts of worm biomass were added to the natural areas. Amphipods in the same habitat exhibited a significant difference in the three treatments (Table 18). Further analysis indicated that the predicted line was different from either of the measured treatments (Table 19). While the natural predation and no predator values were not significantly different overall, differences were evident during certain time intervals (Table 19 and Fig. 14). Values predicted by the model indicated that amphipod populations should decrease to zero at the predation levels suggested by laboratory studies.

In unvegetated open water areas, there were significant differences between treatments for polychaete biomass (Table 20). The predicted line differed from both natural and predation values, but the latter two did not differ from each other (Table

21). The natural and no predation levels of polychaete biomass frequently did not differ from each other (Fig. 15). At levels of predation seen in the laboratory, predicted values for shrimp predation consistently decreased over time. Amphipod biomass in the same habitat did not consistently differ between species, although there was significant variation over time (Table 22). Once again, the model predicted biomass values to decrease to zero (Fig. 16). By days 42 and 56, there was significantly less mass of amphipods in cores taken outside the cages versus inside the cages.

At the time of the last two samplings for each habitat, there were differences in the abundances of the dominant species of polychaetes and amphipods (Table 23). In the vegetated areas at day 56 (the last day both habitats were sampled), Streblospio benedicti and Corophium louisianum greatly increased in abundance inside the cages. Melinna maculata decreased in the absence of predation (Figs. 17 and 18). In nonvegetated areas at day 56, Streblospio benedicti again increased in abundance, but Ampelisca abdita was the dominant amphipod within the cages (Figs. 19 and 20).

Table 14. Calculation of removal rate of polychaetes per day by brown shrimp using natural densities from a surface area of 78.5 cm² representing the coring device used in sampling. Marsh calculations (A) take into account the amount of time water was present on the surface during each two week interval of time. Such correction was not necessary for the open water values (B). Consumption rates per day per shrimp were values calculated from growth studies.

A. Marsh surface

Interval of time	Density of shrimp per core #/78.5 sq. cm.	Consumption g/day/shrimp	Optimal removal rate
A	0.031554	0.0054581	0.00017222
B	0.0412468	0.0054581	0.00022513
C	0.05094	0.0054581	0.00027804
D	0.060633	0.0054581	0.00033094
E	0.070326	0.0054581	0.00038385

Interval of time	% time marsh surface was flooded	Removal rate given marsh access
A	0.78333	0.000134909
B	0.77083	0.000173536
C	0.99405	0.000276381
D	0.98809	0.000326999
E	1	0.000383846

B. Open bottom

Interval of time	Density of shrimp per core #/78.5 sq. cm.	Consumption g/day/shrimp	Optimal removal rate
A	0.084024	0.0054581	0.00045861
B	0.0738946	0.0054581	0.00040332
C	0.0637652	0.0054581	0.00034804
D	0.0536359	0.0054581	0.00029275

Table 15. Calculation of removal rate of amphipods per day by natural densities of brown shrimp from a surface area of 78.5 cm² representing the coring device used in sampling. Marsh calculations (A) take into account the amount of time water was present on the surface during each two week interval of time. Such correction was not necessary for the open water values (B). Consumption rates per day per shrimp were calculated from data collected from growth studies.

A. Marsh surface

Interval of time	Density of shrimp per core #/78.5 sq. cm.	Consumption g/day/shrimp	Optimal removal rate
A	0.031554	0.0073412	0.00023164
B	0.0412468	0.0073412	0.0003028
C	0.05094	0.0073412	0.00037396
D	0.060633	0.0073412	0.00044512
E	0.070326	0.0073412	0.00051628

Interval of time	% time marsh surface was flooded	Removal rate given marsh access
A	0.78333	0.000181454
B	0.77083	0.000233408
C	0.99405	0.000371736
D	0.98809	0.000439818
E	1	0.000516277

B. Open bottom

Interval of time	Density of shrimp per core #/78.5 sq. cm.	Consumption g/day/shrimp	Optimal removal rate
A	0.084024	0.0073412	0.00061684
B	0.0738946	0.0073412	0.00054248
C	0.0637652	0.0073412	0.00046811
D	0.0536359	0.0073412	0.00039375

Table 16. Description of formula and definition of terms used in calculation of theoretical effects of juvenile brown shrimp feeding on infauna in the absence of other predators.

The theoretical density of infauna at time t was taken to be:

$$N_t = N_{t-1} + (C_n * t)$$

where:

N_t = dry weight of infauna at time t

N_{t-1} = dry weight of infauna at the beginning of the two week period in question

C_n = net change in infauna = $C_c - P$

C_c = change in infauna inside of cage, no predators

P = infauna lost to predation (recalculated each 14 day interval to account for changes in predator density)

Table 17. Results of repeated measures analysis of variance (ANOVA) comparing the change in the dry weight of polychaetes in vegetated areas among natural cores of sediment, cores from inside predator exclusion cages, and a theoretical line predicting the effects of the feeding of brown shrimp alone.

Dependent variable: dry weight of polychaetes (log transformed)

Tests of hypotheses for between subject effects

Source	d.f.	Type III S.S.	Mean Square	F Value	P Value
treatment	2	0.00053499	0.00026749	1.78	0.2028
error	15	0.00225658	0.00015044		

Tests of hypotheses for within subject effects

Source	d.f.	Type III S.S.	Mean Square	F Value	P Value
time	5	0.00079379	0.00015876	1.98	0.0906
time*treatment	10	0.0011748	0.00011748	1.47	0.1681
error	75	0.00599937	0.00007999		

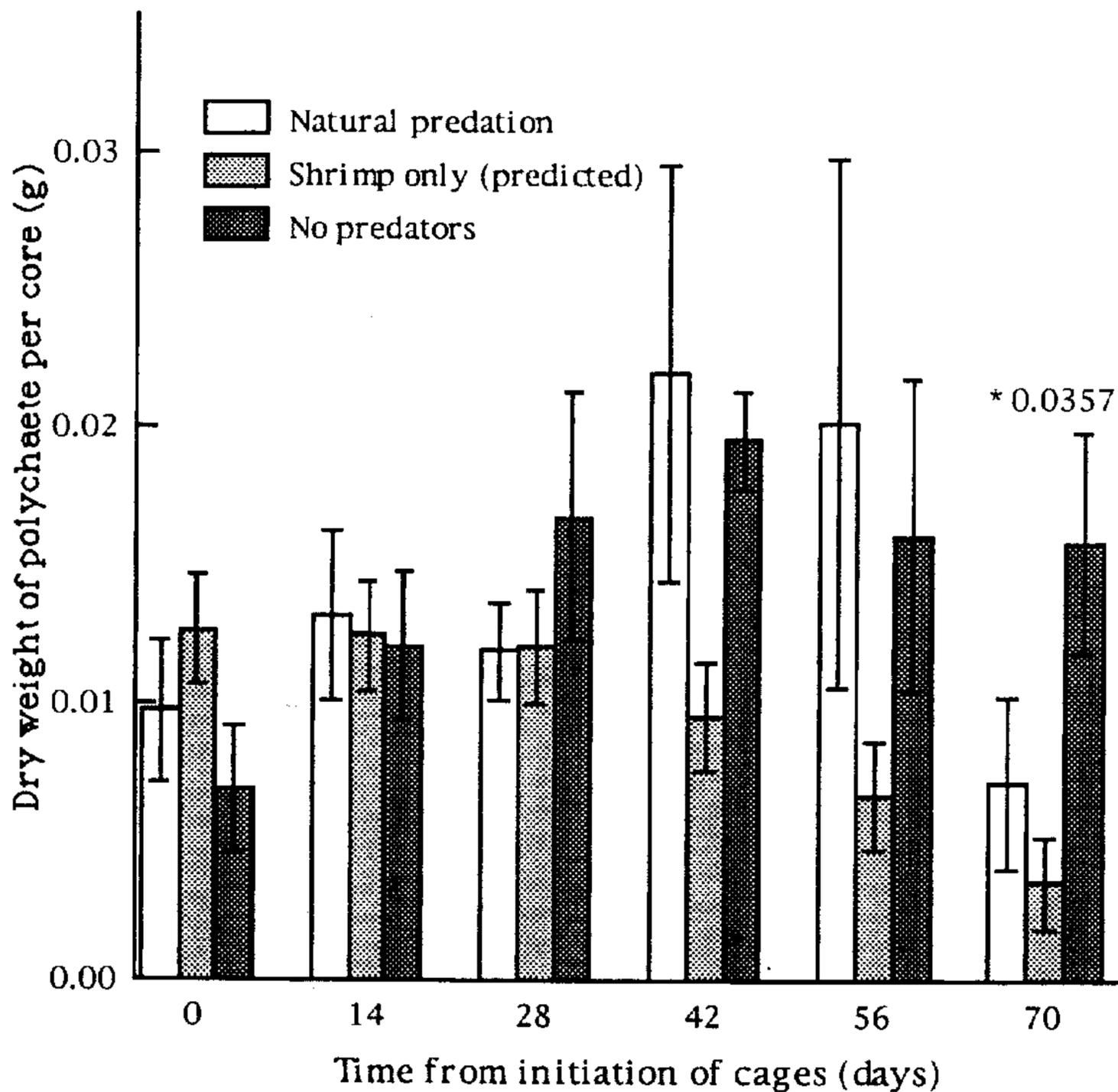


Figure 13. A comparison of change in polychaete biomass (dry weight) per experimental core (78.5 cm²) over time for three predation treatments in vegetated marsh areas. Natural predation refers to cores of sediment collected outside predator exclusion cages. No predation cores were collected inside the cages. The predicted shrimp only predation values were calculated. Error bars indicated one standard error. Numbers placed over some intervals indicate p-value of ANOVA comparing treatments within a time period.

Table 18. Results of repeated measures analysis of variance (ANOVA) comparing the change in the dry weight of amphipods in vegetated areas among natural cores of sediment, cores from inside predator exclusion cages, and a theoretical line predicting the effects of the feeding of brown shrimp alone. An asterix indicates significant differences at the $\alpha = 0.05$ level.

Dependent variable: dry weight of amphipods (log transformed)

Tests of hypotheses for between subject effects

Source	d.f.	Type III S.S.	Mean Square	F Value	P Value
treatment	2	0.00022809	0.00011404	4.88	*0.0234
error	15	0.00035087	0.00002339		

Tests of hypotheses for within subject effects

Source	d.f.	Type III S.S.	Mean Square	F Value	P Value
time	5	0.00005717	0.00001143	0.81	0.5441
time*treatment	10	0.00019177	0.00001918	1.36	0.2139
error	75	0.00105486	0.00001406		

Table 19. Contrasts constructed from ANOVA procedures comparing levels of amphipod biomass (dry weight per experimental core) between predation treatments in vegetated marsh areas. Natural predation refers to cores collected in areas without predator restrictions. No predation cores were collected inside cages which excluded epibenthic and nektonic organisms. Predicted shrimp predation are values calculated to potentially represent feeding of only brown shrimp in the same area. An asterix indicates significant differences at the $\alpha = 0.05$ level.

Treatment	F value	p-value
Natural predation vs. predicted shrimp pred.	6.57	*.0121
Natural predation vs. no predation	1.38	0.2435
Predicted shrimp predation vs. no predation	13.96	*0.0003

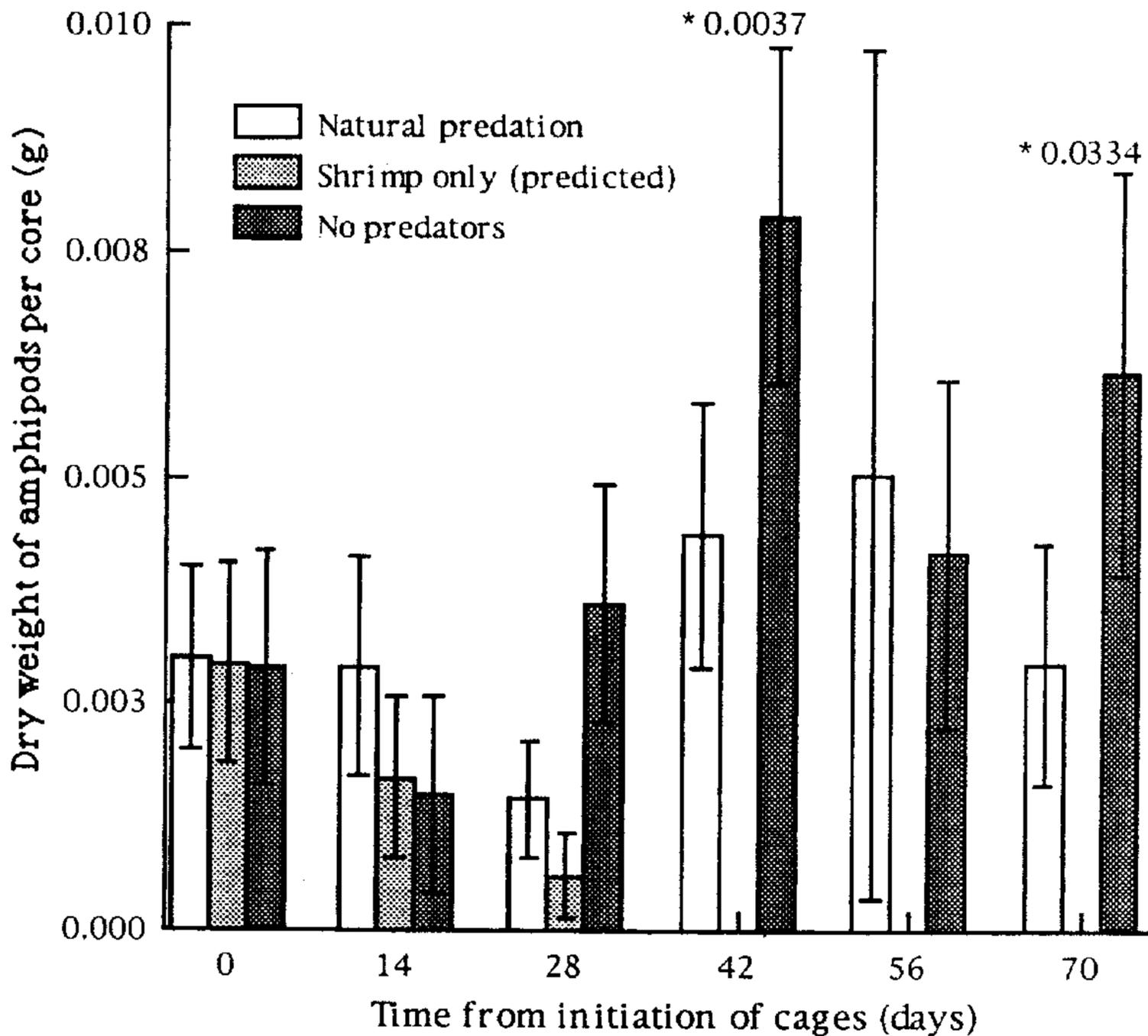


Figure 14. A comparison of change in amphipod biomass (dry weight) per experimental core (78.5 cm^2) over time for three predation treatments in vegetated marsh areas. Natural predation refers to cores of sediment collected outside predator exclusion cages. No predation cores were collected inside the cages. The predicted shrimp only predation values were calculated. Error bars indicated one standard error. Numbers placed over some intervals indicate p-value of ANOVA comparing treatments within a time period.

Table 20. Results of repeated measures analysis of variance (ANOVA) comparing the change in the dry weight of polychaetes in unvegetated areas among natural cores of sediment, cores from inside predator exclusion cages, and a theoretical line predicting the effects of the feeding of brown shrimp alone. An asterix indicates significant differences at the $\alpha = 0.05$ level.

Dependent variable: dry weight of polychaetes (log transformed)

Tests of hypotheses for between subject effects

Source	d.f.	Type III S.S.	Mean Square	F Value	P Value
treatment	2	0.00125353	0.00062676	4.5	*0.0309
error	14	0.00194784	0.00013913		

Tests of hypotheses for within subject effects

Source	d.f.	Type III S.S.	Mean Square	F Value	P Value
time	4	0.00017747	0.00004437	0.62	0.6485
time*treatment	8	0.00086138	0.00010767	1.51	0.1745
error	56	0.00399233	0.00007129		

Table 21. Contrasts constructed from ANOVA procedures comparing levels of polychaete biomass (dry weight per experimental core) between predation treatments in nonvegetated areas. Natural predation refers to cores collected in areas without predator restrictions. No predation cores were collected inside cages which excluded epibenthic and nektonic organisms. Predicted shrimp predation are values calculated to potentially represent feeding of only brown shrimp in the same area. An asterix indicates significant differences at the $\alpha = 0.05$ level.

Treatment	F value	p-value
Natural predation vs. predicted shrimp pred.	11.95	*0.0009
Natural predation vs. no predation	0.02	0.8805
Predicted shrimp predation vs. no predation	10.49	*0.0018

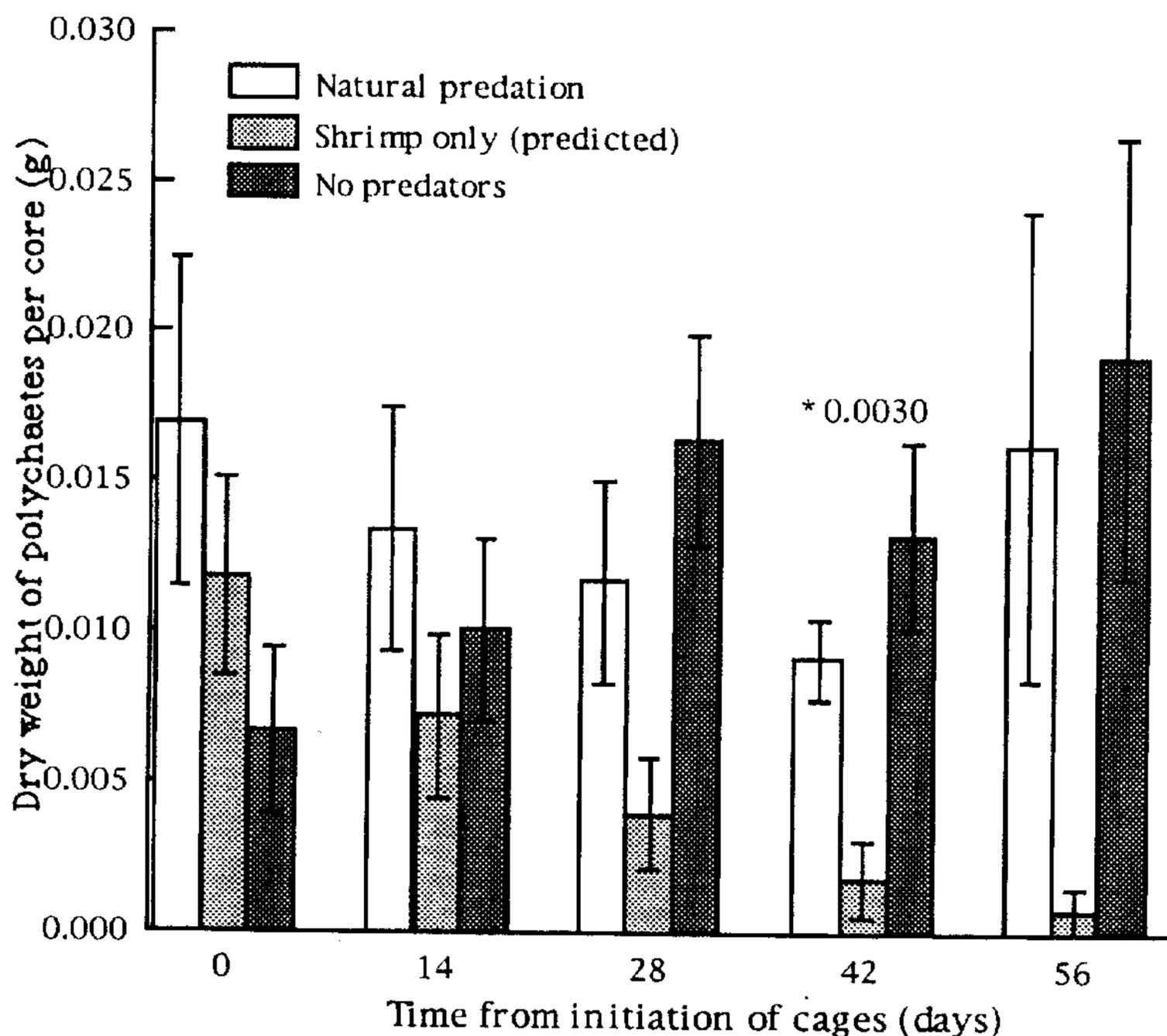


Figure 15. A comparison of change in polychaete biomass (dry weight) per experimental core (78.5 cm²) over time for three predation treatments in open water areas. Natural predation refers to cores of sediment collected outside predator exclusion cages. No predation cores were collected inside the cages. The predicted shrimp only predation values were calculated. Error bars indicated one standard error. Numbers placed over some intervals indicate p-value of ANOVA comparing treatments within a time period.

Table 22. Results of repeated measures analysis of variance (ANOVA) comparing the change in the dry weight of amphipods in unvegetated areas among natural cores of sediment, cores from inside predator exclusion cages, and a theoretical line predicting the effects of the feeding of brown shrimp alone. An asterix indicates significant differences at the $\alpha = 0.05$ level.

Dependent variable: dry weight of amphipods (log transformed)

Tests of hypotheses for between subject effects

Source	d.f.	Type III S.S.	Mean Square	F Value	P Value
treatment	2	0.00053429	0.00026714	3.59	0.0552
error	14	0.00104244	0.00007446		

Tests of hypotheses for within subject effects

Source	d.f.	Type III S.S.	Mean Square	F Value	P Value
time	4	0.00052832	0.00013208	6.14	*0.0004
time*treatment	8	0.00019656	0.00002457	1.14	0.3499
error	56	0.00120393	0.0000215		

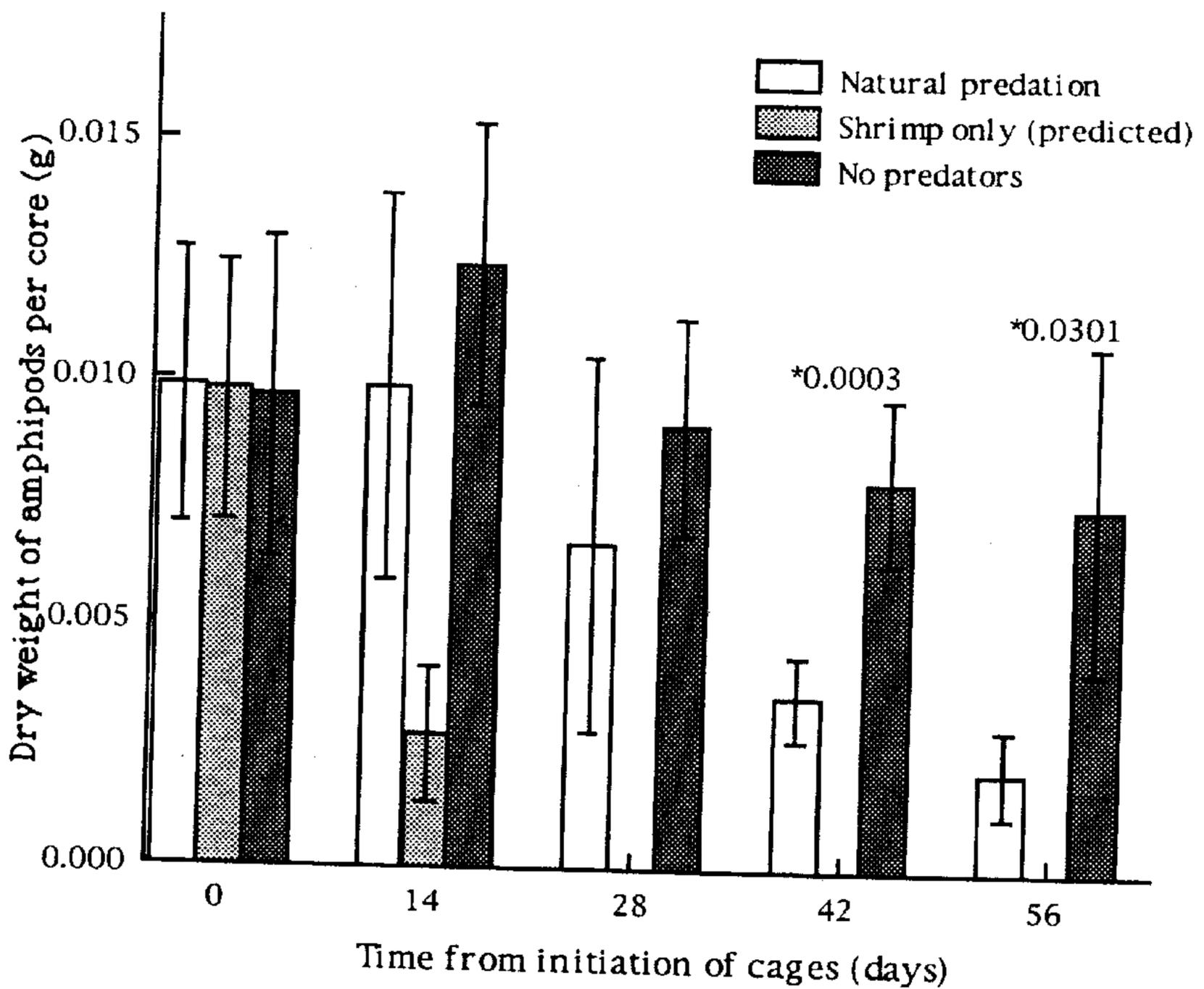


Figure 16. A comparison of change in amphipod biomass (dry weight) per experimental core (78.5 cm^2) over time for three predation treatments in open water areas. Natural predation refers to cores of sediment collected outside predator exclusion cages. No predation cores were collected inside the cages. The predicted shrimp only predation values were calculated. Error bars indicated one standard error. Numbers placed over some intervals indicate p-value of ANOVA comparing treatments within a time period.

Table 23. Abundances of dominant species of polychaetes and amphipods collected in cores (78.5 cm²) from inside predator exclusion cages (no predation) and outside the cages (natural predation). Means are given and are followed by the standard error in parentheses. Day refers to the number of days elapsed since the initiation of the caging study.

A. Marsh Surface

	Natural Pred. 4/30/91 Day 56	No Pred. 4/30/91 Day 56	Natural Pred. 5/14/91 Day 70	No Pred. 5/14/91 Day 70
<u>Capitella capitata</u>	21.2 (12.5)	14.7 (5.5)	13.0 (6.4)	17.8 (5.7)
<u>Streblospio benedicti</u>	53.5 (19.5)	150.2 (36.7)	44.5 (11.1)	308.7 (105.5)
<u>Melinna maculata</u>	14.3 (11.0)	0.3 (0.3)	0.5 (0.3)	0.7 (0.3)
<u>Grandiderella bonneroides</u>	0.7 (0.5)	5.2 (4.2)	3.0 (1.6)	9.3 (3.1)
<u>Ampelisca abdita</u>	1.5 (0.7)	1.3 (0.5)	1.2 (0.8)	6.0 (2.3)
<u>Gammarus mucronatus</u>	0.2 (0.2)	1.0 (0.5)	16.8 (8.5)	3.2 (2.4)
<u>Corophium louisianum</u>	1.8 (1.3)	81.8 (39.6)	2.5 (1.1)	92.7 (37.5)

B. Open Bottom

	Natural Pred. 4/16/91 Day 42	No Pred. 4/16/91 Day 42	Natural Pred. 4/30/91 Day 56	No Pred. 4/30/91 Day 56
<u>Capitella capitata</u>	9.2 (4.3)	3.4 (0.3)	11.7 (7.7)	9.6 (3.9)
<u>Streblospio benedicti</u>	38.5 (8.3)	58.2 (22.1)	20.2 (5.1)	58.4 (18.3)
<u>Melinna maculata</u>	1.83 (1.1)	5.4 (1.8)	3.7 (1.0)	3.0 (0.9)
<u>Grandiderella bonneroides</u>	8.2 (4.1)	16.4 (13.3)	1.7 (1.3)	1.0 (0.8)
<u>Ampelisca abdita</u>	36.3 (9.1)	109.2 (25.1)	26.0 (10.2)	120.0 (62.6)
<u>Gammarus mucronatus</u>	3.2 (1.7)	1.2 (0.8)	0.3 (0.2)	0.0 (0.0)
<u>Corophium louisianum</u>	9.8 (4.5)	6.0 (3.8)	1.2 (1.0)	25.4 (24.2)

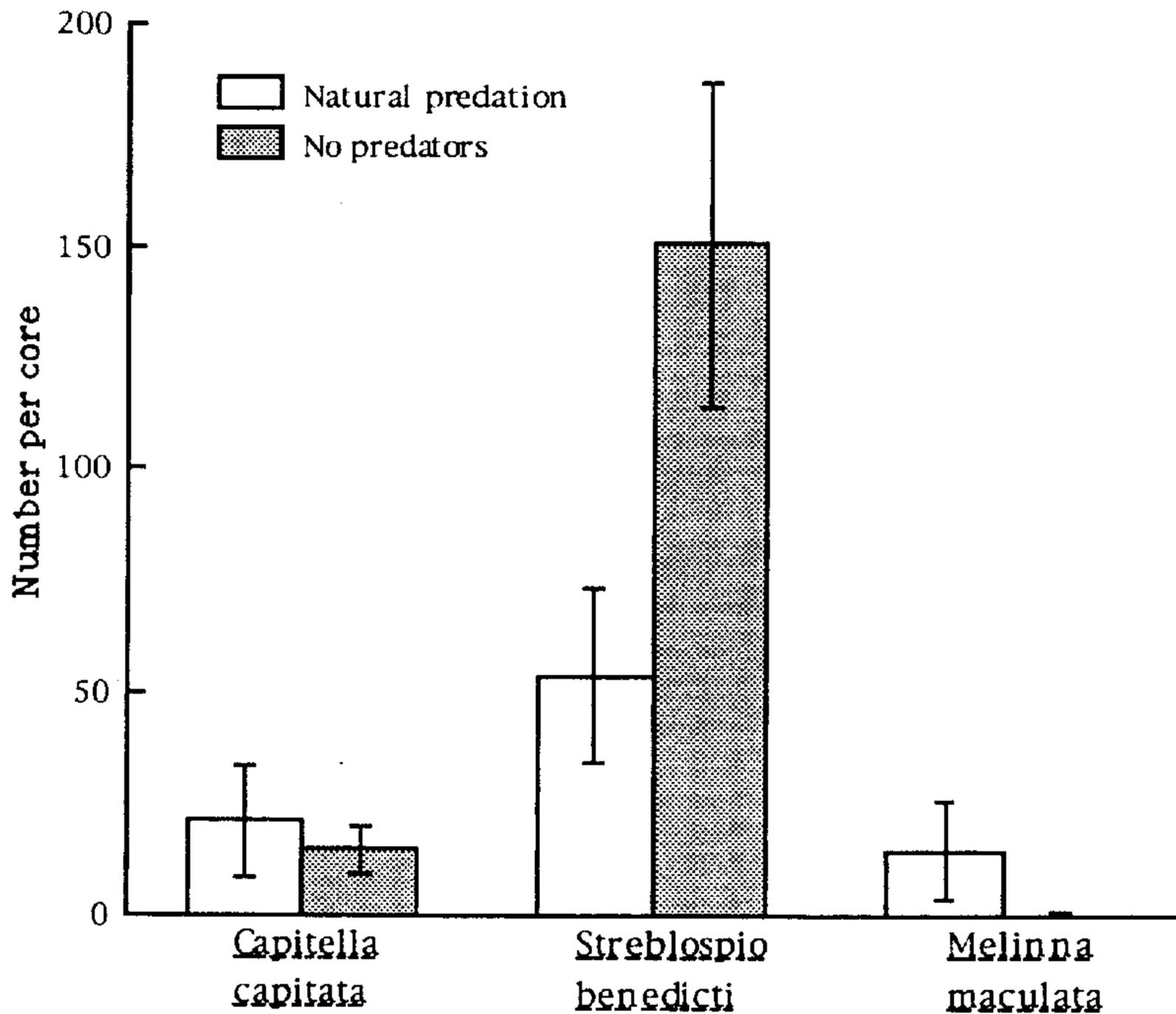


Figure 17. A comparison of numerically dominant polychaete species inside and outside predator exclusion cages constructed on the marsh surface. Natural predation refers to cores collected outside each cage and no predators to those collected inside each cage. The surface area of the sediment collected in each core was 78.5 cm².

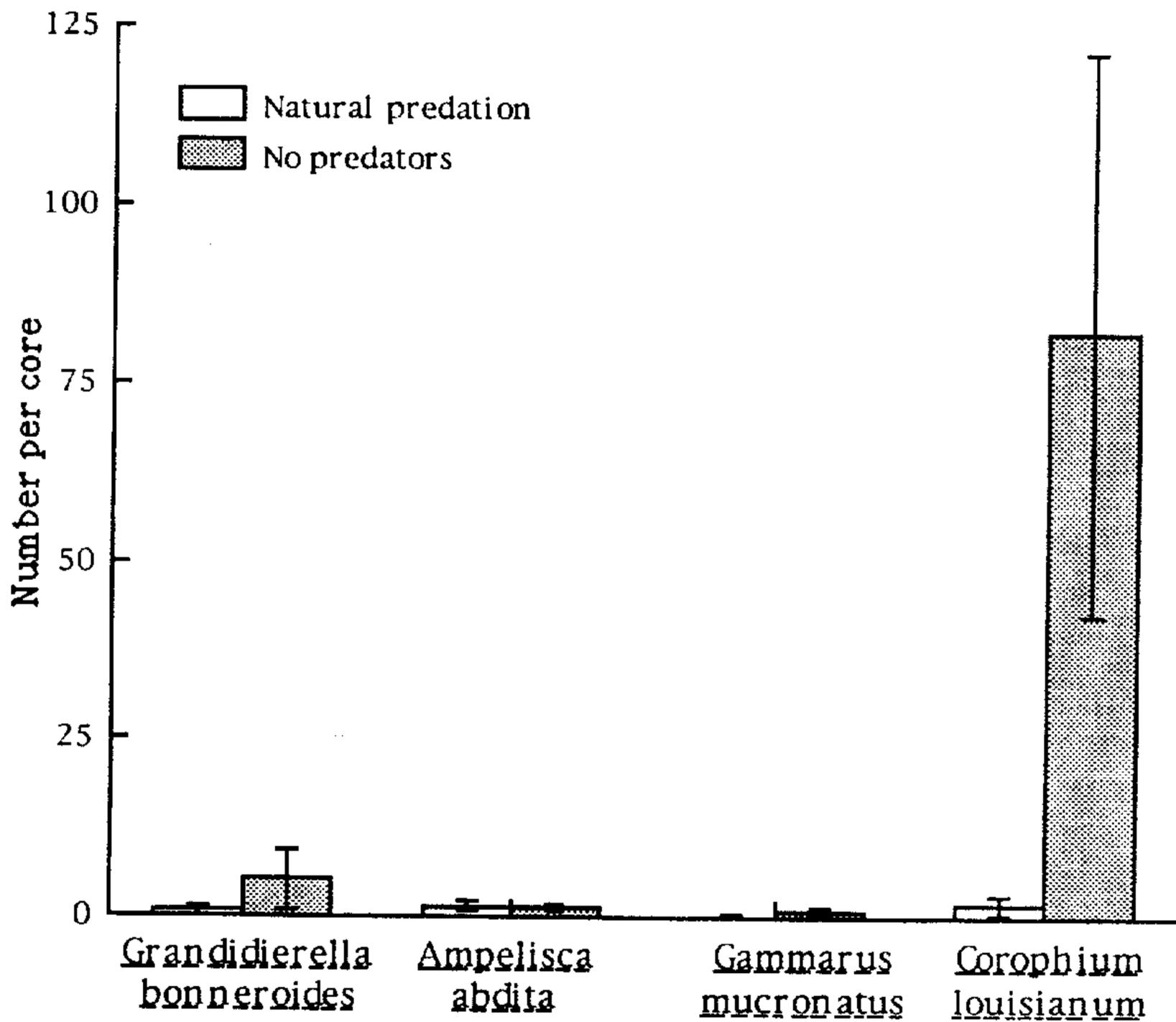


Figure 18. A comparison of numerically dominant amphipod species inside and outside predator exclusion cages constructed on the marsh surface. Natural predation refers to cores collected outside the cages and no predators to those collected inside the cages. The surface area of the sediment collected in each core was 78.5 cm².

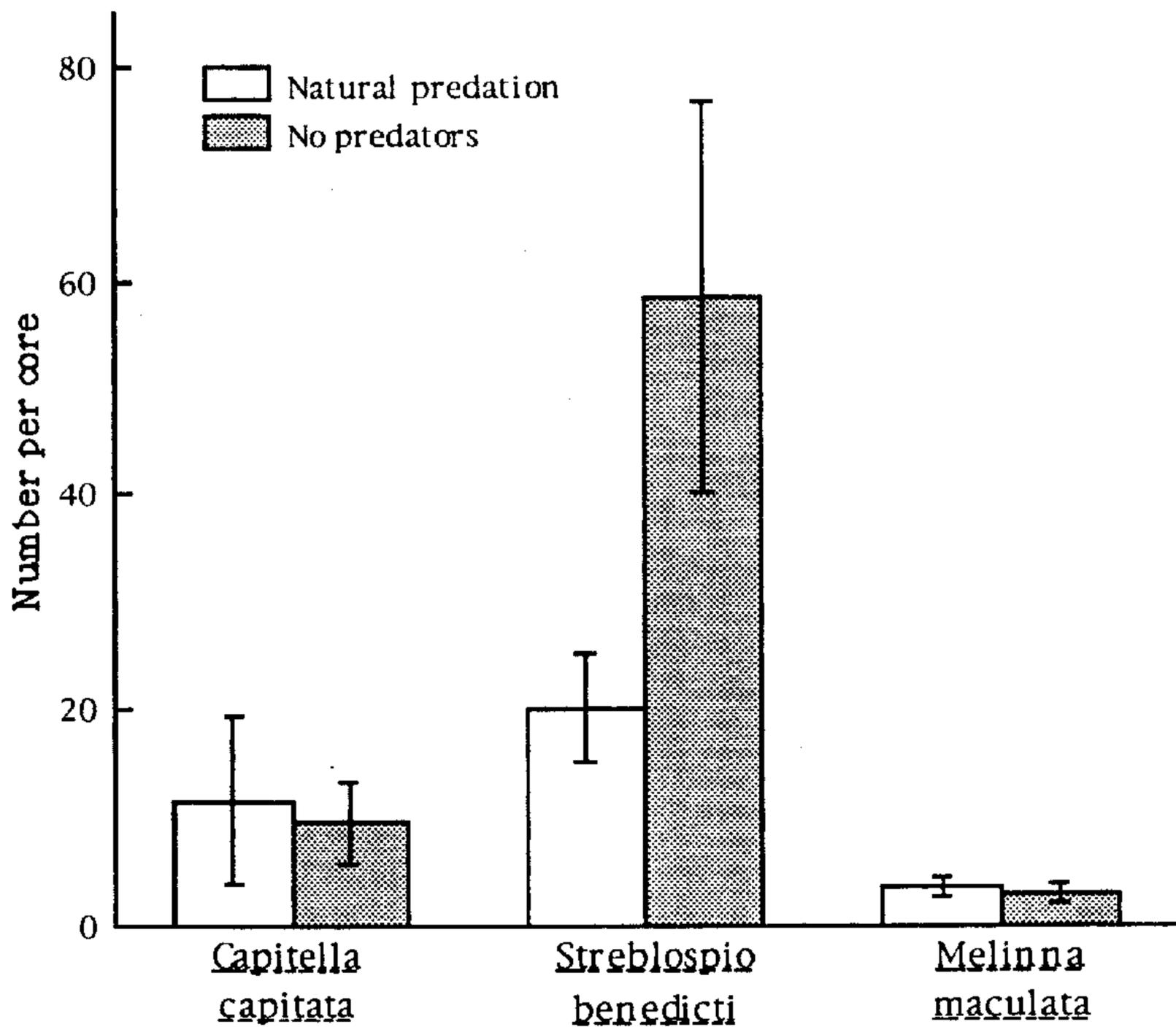


Figure 19. A comparison of numerically dominant polychaete species inside and outside predator exclusion cages constructed over unvegetated bottom. Natural predation refers to cores collected outside each cage and no predators to those collected inside each cage. The surface area of the sediment collected in each core was 78.5 cm².

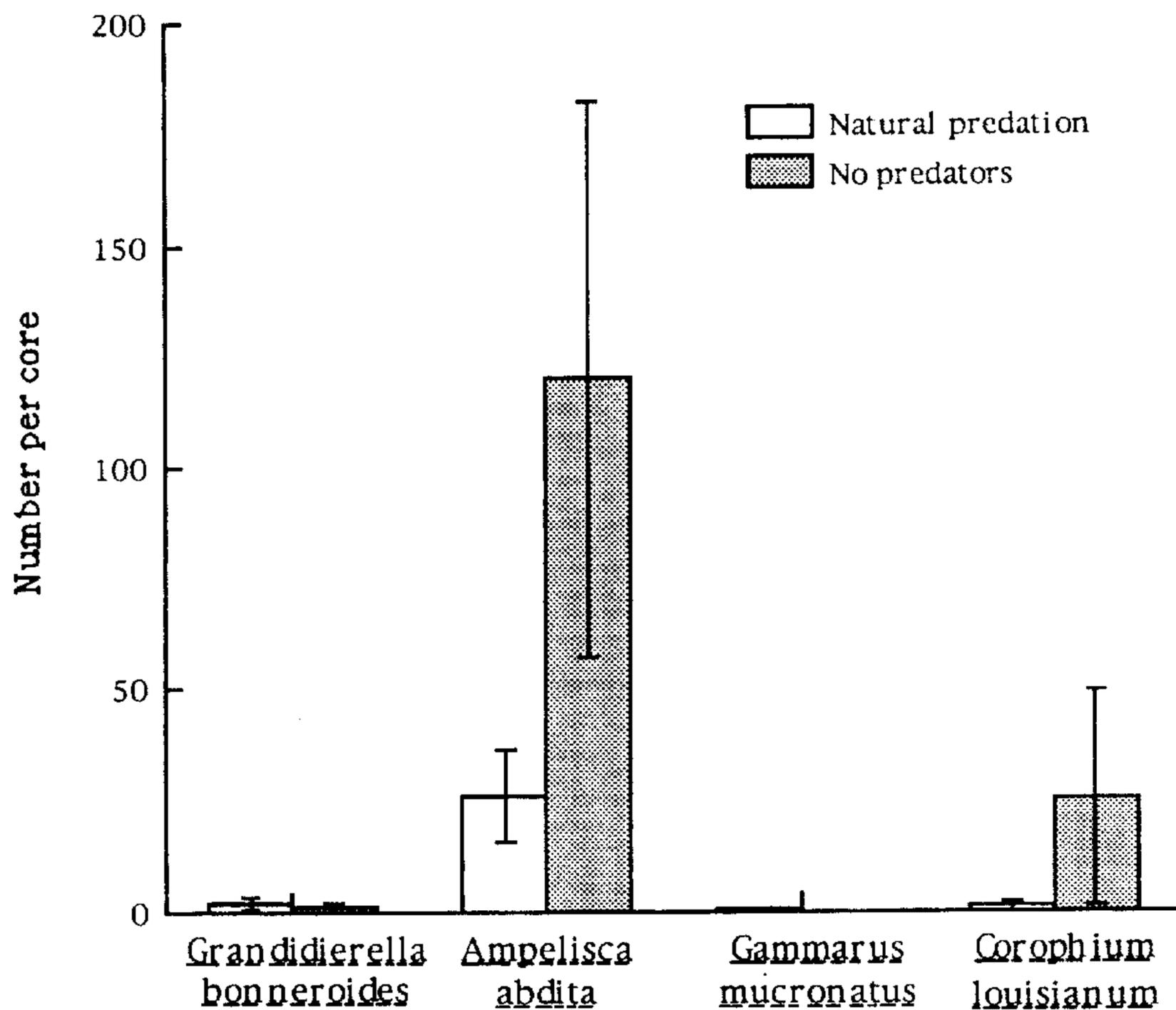


Figure 20. A comparison of numerically dominant amphipod species inside and outside predator exclusion cages constructed over unvegetated bottom. Natural predation refers to cores collected outside each cage and no predators to those collected inside each cage. The surface area of the sediment collected in each core was 78.5 cm².

DISCUSSION

Circumstantial evidence indicates possible dietary differences between juvenile Penaeus aztecus and Penaeus setiferus. While their basic life cycles are quite similar, the brown shrimp occurred at times and places coinciding with higher abundances of infauna, particularly polychaetes. Brown shrimp enter marsh areas in the early spring when infaunal populations are frequently at their yearly peak. During the first weeks of residence, there is often no significant difference in the distribution of brown shrimp between the intertidal marsh surface and nonvegetated, subtidal areas (Zimmerman and Minello 1984; Zimmerman et al. 1984; Minello and Zimmerman 1985). Importantly, it is at this time that the least difference occurs in infaunal densities between the two habitats. As time passes and infaunal levels in open water decline relative to the marsh, brown shrimp are found more frequently on the marsh surface with its higher abundance of worms. By contrast, the white shrimp immigrate into bays during the summer when infauna are already reduced and often distribute without regard to habitat type.

Brown and white shrimp differed significantly in their ability to remove infauna from sediment (Fig. 1). During both early and late seasonal runs of the experiment, P. aztecus significantly reduced the abundance of certain polychaetes, such as spionids, (Tables 1 and 2) identified as superficial burrowers (D. Harper, pers. comm.; see Fauchald and Jumars 1979 for

review). Tubicolous crustaceans were significantly removed from the sediment during February when abundances were high, but not during May when abundances were low (Table 3, Figs. 2 and 3). During corresponding experiments using P. setiferus, no group of infaunal organisms was significantly reduced in abundance (Table 4, Figs. 4 and 5). In experiments conducted by Service et al. (1992), white shrimp did not deplete the total number of macroinfauna, nor Streblospio benedicti specifically, in sediment from a South Carolina estuary. They did, however, note a decrease in Capitella abundances between treatment and control samples. This difference was not highly significant and might be caused by a factor other than shrimp feeding, including natural spatial variability in worm distribution (Kneib 1984).

Worms that live deeper in the sediment, such as capitellids, were not affected by brown shrimp. Similarly, species of crustaceans that were reduced during the February run of the experiment were all superficial tube dwellers. This result may be due to physical limitations of how deep in the sediment the brown shrimp can forage as predators. Shrimp are demersal and feed by browsing and digging through surface sediments. P. aztecus or any other shrimp can only successfully exploit and affect populations of near-surface infauna. Feeding differences between species of shrimp may be related to their ability to dig. Organisms such as capitellids appear to be simply out of reach of most penaeids. Tubicolous crustaceans at the sediment surface, such as the tanaid Hargeria rapax and the amphipod Ampelisca abdita,

also appear to be more available than free-moving species. During laboratory growth studies (discussed later in this section), free swimming amphipods were provided as food to brown shrimp. The predator had difficulty capturing these amphipods, as they swam quickly around the container. In nature, tubicolous organisms would be limited in their range of movement and may be more easily located and captured than free-moving organisms.

Thus, differential selection of prey from sediment by brown shrimp has major implications to infaunal community structure and shrimp production dynamics. Marshes vary widely in species composition in terms of infauna and densities of those species present. This can be related to many factors, such as salinity regime or nutrient levels. Moreover, overall abundance of infauna may be misleading as evidence of the quality of foraging area for brown shrimp. A marsh dominated by deep dwelling capitellids may seem similar in terms of infaunal density or biomass to a marsh or other area inhabited primarily by spionids. But to Penaeus aztecus, these areas are very different; one situation allows little or no access to the prey, while the other offers food in abundance. This may translate into local success or failure of brown shrimp productivity, yet such fine scale habitat differences are rarely if ever considered.

During the two trial periods tested for brown shrimp, there were some differences among groups the penaeid could successfully remove from the substrate (Table 2). Notably, no crustaceans were affected during May, although three species

were reduced during February. Similarly, Melinna maculata and oligochaetes were reduced during the former and not the latter trial. The cause, most obviously, and perhaps most significantly, was that densities of infauna differed greatly during the two periods. Control cores collected February 27 had an averaged 171.4 organisms per core (standard error = 20.0, core area = 78.54 cm²) representing the period before the annual infaunal decline. By May 5th, the mean abundance was 84.7 organisms per core (standard error = 17.6). Melinna maculata changed from an average density of 15.8 per control core (standard error = 2.0) in February to less than one per control core (mean = 0.6, standard error = 1.0). These prey during the later period may have been simply more difficult to locate. In addition, the abundances may have been too low to achieve statistical significance upon removal.

White shrimp did not significantly affect any of the infaunal groups in question (Table 4, Figs. 4 and 5). This is despite their highly limited access to any other food items. Further, after the four day exposure to the sediment, white shrimp had gained much less weight than did brown shrimp (Fig. 6). The pattern held true for both early and late season trials of the experiment. Late in their residence period, white shrimp actually lost weight when allowed to feed from marsh surface sediment. One might assume that after a period of time, a starving animal would make use of food resources normally outside its dietary breadth. White shrimp either consumed something in the core not measured (edaphic algae?) or they are poorly equipped to dig up and

capture infauna. Perhaps in their digging, they do not to penetrate the sediment surface to a sufficient degree to capture infauna. Either hypothesis corresponds with distributional and temporal patterns known for white shrimp, although it is unlikely that much of their preferred food was available as they gained little or no weight.

Brown shrimp survived longer than did white shrimp overall and lived longer when fed animal material alone or in combination with Skeletonema (Tables 5 and 6, Fig. 7). Both species of penaeids survived longer on diets that incorporated animal material over algae alone (Tables 7 and 8). Brown shrimp appeared to have higher survival rates, but grew less, when fed amphipods versus polychaetes. Does this indicate that amphipods are a higher quality food source? This result is more likely an artifact of the container system used in the experiments and the habits of the worms themselves. When polychaetes are removed from protective material such as sediment or detritus, they writhe about and secrete mucus in an attempt to burrow or cover themselves. Large numbers of worms in a limited area can very quickly degrade the quality of the sea water. Worms were introduced daily to the 800 ml beakers holding the shrimp. The aim was to provide enough prey that some would be left the next day, and thus would be constantly available. The difficulty was that more than one or two remaining worms often resulted in yellow water with a scum-like layer on the surface. The loss of shrimp in the polychaete based treatments appear to be related to

these occasional fouling events. In any subsequent studies using polychaetes as food, larger containers should be used and the water partially changed daily.

Additional mortality was present in the worm treatments due to increased activity of the shrimp. Penaeids that were fed polychaetes or polychaetes plus algae were much more active than those in other treatments, including amphipods. As a result, they were more likely to jump above the water line and adhere themselves to the sides of the beaker. Polychaete fed shrimp also jumped out of their beakers entirely, despite the plastic wrap covering the opening. There were two small holes in the plastic for aeration and addition of food and the shrimp on occasion exited through these openings. Survival data, then, is confounded by these factors. To compare the relative quality of the faunal diets, growth of the shrimp was the best measure used.

Brown shrimp and white shrimp differed in their growth response to the diets and the magnitude of that difference increased over time (Tables 9 and 10, Figs. 8 and 9). Penaeus aztecus consistently grew at a greater rate than did P. setiferus on the diets provided. This is contrary to evidence from the field and laboratory that suggests that white shrimp grow more quickly than do brown shrimp (Johnson and Fielding, 1956; Wheeler, 1968; Knudsen et al., 1977). This discrepancy may be related to the restricted diets provided during this study. Penaeids feeding in cages in the field have access to a wide variety of food sources and are more likely to encounter their preferred food source. The

diets provided appear to have been lacking in some way for the white shrimp as maximum growth rates observed in nature were not achieved. Experimental brown shrimp growth, on the other hand, was similar to that observed in nature.

Polychaete-based diets consistently produced more growth in brown shrimp than in white shrimp (Table 11). Amphipods were a poor diet for both species, producing little growth regardless of whether algae were present (Tables 12 and 13, Figs. 10 and 11). The consumption of amphipods by brown shrimp under laboratory conditions has been taken to indicate that the penaeid is an important predator of these animals in the field (Nelson 1979). While the shrimp may be potentially significant in the structuring of the infaunal population, amphipods would seem of secondary importance in a penaeid's diet. Brown shrimp consistently consumed more of the fauna provided in the combination treatments (Fig. 12), although neither species ate as many amphipods by weight as they did polychaetes. White shrimp may have utilized the diatoms present.

Incremental growth values in the current research fall well below those reported for brown and white shrimp fed Artemia and Skeletonema under a similar experimental system (McTigue and Zimmerman, 1991). This difference can be viewed in several ways. First, Artemia nauplii during the first few days of life are nutrient rich, still harboring yolk reserves. Second, they may resist capture to a lesser degree than polychaetes and amphipods, resulting in less energy expenditure by the predator. The

difference in growth rates for brown shrimp may be significant, but it in no way approaches the contrast seen in the white shrimp. In the current research, between days 20 and 25 white shrimp added an average of 0.0278 g (standard error = 0.0050) when fed polychaetes and Skeletonema. The change in weight resulting from an Artemia and Skeletonema diet between days 20 and 24 was approximately 0.17 g. This suggests that through some nutritional or behavioral advantage, brine shrimp may more closely approximate the white shrimp natural, but unknown, faunal food source than do infauna.

One potential faunal food source for juvenile white shrimp may be estuarine mysids. These small, shrimp-like crustaceans have been identified in the proventriculus of several species of penaeids (Chong and Sasekumar 1981; Suthers 1984). Penaeus plebejus, in a sample from Sydney Harbor, Australia, had guts filled almost entirely with the mysid Rhopalophthalmus dakini (Suthers 1984). While they have not been reported from the guts of white shrimp, mysids are very common in marshes and adjacent open bottom areas, including the areas sampled in this study. Their absence from white shrimp guts may be due to trituration by the penaeids' gastric mill. Further, white shrimp held in aquaria often can be seen hovering in the water column (Z. Zein-Eldin, pers. comm.) and may be capturing food there. Tanaids are a potential food source based on work done in Georgia salt marshes (R. Kneib, pers. comm.). In Texas, however, tanaid abundances during the residence period of white shrimp are low.

It is not conceivable that in this marsh system tanaids could support an abundance of shrimp in the summer.

Marshes have long been considered important to penaeid populations. These areas can vary in many respects including accessibility of the marsh surface and presence of potential prey. While many areas are classified as salt marshes, they may be lacking in the basic requirements for success of penaeid populations. It is important to understand the basic biology of animals to draw a more complete picture of their role in a particular ecosystem.

Wenner and Beatty (1993) compared shrimp densities and catch statistics from salt marshes and the near shore waters of South Carolina with those published for Texas by Zimmerman and others. They found that although South Carolina had much more extensive marshes, penaeids were found in greater densities in Texas waters. This held true for the in situ measurements as well as the commercial landings. It was suggested that the less reticulated eastern marshes with their 1.5 m tides offered less access to the marsh surface for penaeids than those in the Gulf, resulting in higher mortality rates due to increased predation pressure. I postulate that predation is only one possible mechanism influencing shrimp populations in these areas. Limited access to the marsh surface would also affect availability of potential food items. A marsh with great tidal exchange and little edge area would offer less actual foraging time on the infauna-rich marsh surface. Instead of residing in stands of high

water as seen in the northwestern Gulf, the shrimp in South Carolina marshes would spend significant amounts of time migrating back and forth with ebb and flood waters. Further, for several hours each day penaeids would be limited to tidal creeks with high levels of competition for limited resources, as well as increased predation rates. In the same paper, Wenner and Beatty indicated that the numerically dominant penaeid in South Carolina marshes is the white shrimp. In the marshes of Galveston Bay, brown shrimp are more common than either white or pink shrimp. I believe that the difference in dominant species may be related to food resources available in the respective areas. In South Carolina, the dominant penaeid is the one that does not significantly select for the marsh surface and may make little use of infaunal resources. As a result, white shrimp can prosper in an area with limited marsh access. In Texas, brown shrimp, which are infaunal feeders, are dominant in marshes that allow ample access to areas densely populated by their potential prey. Predation may play a role in overall population levels, but the dominance of one species over the other correlates well with what is known of their trophic dynamics.

Indirect evidence and the feeding studies discussed here make an argument for a strong linkage of brown shrimp to infaunal populations. This predator enters nursery areas when infauna are abundant and moves onto the marsh surface to exploit infaunal populations. Further, my experiments show that brown shrimp can successfully remove infauna from natural substrates.

The types of infauna present in an area may greatly affect the local success of the shrimp, though, and burrowing organisms differ in their availability to the predator. Further, even organisms that the shrimp can catch and consume may vary greatly as food sources, as indicated by differences in growth rates.

White shrimp differ entirely in behavior and feeding compared to brown shrimp. Their spatial and temporal distribution patterns suggest that they do not rely on infaunal populations as the animal element of their omnivorous diet. They, in fact, utilize plants to a greater degree and do not remove burrowing organisms from the substrate. Further, white shrimp do not grow to any significant degree when infauna alone are presented as diets. Whatever the predominant faunal element is in their diets, polychaetes and amphipods do not seem to contribute significantly.

While appearing similar morphologically, P. aztecus and P. setiferus differ greatly in their trophic roles in marsh communities. Brown shrimp are significant predators on infauna for at least part of the animal element of their diets. They also appear to be more carnivorous than are white shrimp. Penaeus setiferus, while co-occurring with P. aztecus during part of their residence period, make little use of infaunal populations as prey and are more herbivorous (McTigue and Zimmerman 1991).

White shrimp appear to derive extensive benefits from feeding on diatoms and other epiphytic microalgae.

At first glance, the simple model of shrimp infauna removal presented here would appear to poorly represent conditions occurring in nature. Further consideration in light of specific dietary choices made by P. aztecus perhaps explain the divergence of theoretical and actual values.

On the vegetated marsh surface, the model predicted a steady decline of polychaete biomass over time (Fig. 13). While the three lines (natural predation, no predation, predicted shrimp feeding alone) were not significantly different statistically (Table 17), some variation in the treatments was evident. The values predicted for shrimp feeding only were similar to those found with natural levels of predation, except for days 42 and 56. At this time both inside and outside the cages there was an increase in worm biomass. By day 70, levels outside the cage were reduced while inside the cages remained elevated. I believe this pattern is due to recruitment to the population (through one of several forms of reproduction). After the initial event, levels outside the cages were cropped back, while in the absence of predation more worms survived. Such settlement events were not built into the model. Overall, though, patterns suggest that penaeid feeding at the rate suggested here, or slightly less, may be significant in regulating polychaete populations within vegetated marsh areas.

For amphipod biomass in the same vegetated habitat, the model predicted that the prey would be grazed back to zero, resulting in significant differences between treatments (Tables 18

and 19, Fig. 14). In nature, though, amphipod populations were highly variable, but clearly present. This implies that the feeding rates seen in the laboratory were much too high. Amphipods, while they were consumed by shrimp both in the selection and growth studies discussed previously, may be consumed to a lesser extent in situ than are polychaetes. The rates of consumption determined in the growth study are probably too high because no alternative prey was offered. Amphipods presented in beakers as prey were more easily captured than those in the field, as well. Cores collected inside the cages appeared to have more amphipods as represented by dry weight than did those from the ambient environment. High degrees of variability, or patchiness, make definitive statements problematic. There is an indication, nonetheless, of a potential settlement event coinciding with that of the worms.

In open bottom areas, there was a significant difference in the three predation treatments in terms of polychaete biomass (Table 20). The model overestimated the amount of material removed by shrimp, resulting in a much lower final biomass (Table 21 and Fig. 15). There is an indication that while there is a great degree of variability, removal by natural predation did not significantly affect the amount of biomass present in the area. An implication of this is perhaps that either the polychaetes are inaccessible to the predators or biomass may be controlled in part by other factors, such as competition within the infauna. Through most of the year, predation may maintain populations in

unvegetated areas at low enough levels that infauna to infauna interactions are of secondary importance. Under conditions of reduced predation, such as inside cages or perhaps during the winter, other structuring forces may become dominant. These include competition, adult-larval interactions, biogenic sediment modifications, among others (Woodin 1976; Peterson 1977; Virnstein 1977; Bell and Coull 1980; Brenchly 1981; Commito 1982; Levin 1982; Kent and Day 1983; Rönn et al. 1988).

In open water habitats, amphipods again were predicted to be rapidly stripped from the substrate. In this case, though, biomass in the natural cores decreased rapidly as well. Due to the high degree of variability in the data, there were no significant differences between the treatments, although there was a significant difference in the biomass levels over time (Table 22 and Fig. 16). Inside the cages (no predation), biomass levels appear to have been maintained at a consistent level. In unvegetated areas there is a lack of structure that may result in easier accessibility of the amphipod to predators and may place infauna in more direct competition with each other. Feeding rates from the lab again overestimated the removal of prey by brown shrimp, probably for the same reasons discussed above. Brown shrimp may consume amphipods from this habitat in the wild, but not at the rate they did when the peracarids were the only prey available.

Since brown shrimp select for certain infaunal organisms when feeding over natural substrates, it seems reasonable to

consider what species of infauna were affected by the lack of predation. Three species of polychaetes and four species of amphipods dominated numerically, although a wide variety of other worms were known to occur (Table 23). Abundances at day 56 of the caging experiment were compared because this was the last point at which both habitats were sampled. On the marsh surface, Streblospio benedicti and Corophium louisianum responded with the greatest increase in abundance of all infauna to the removal of predation (Figs. 17 and 18). Very importantly, these are organisms that live at or near the surface and were significantly reduced by brown shrimp when abundant. Variability for Corophium, a tube dweller, was very great because these amphipods would occur in large colonial patches. These patches were unequally distributed spatially and were not always sampled by random coring. Capitella capitata, a deeper burrower, did not respond to the construction of predator exclusion devices. Melinna maculata, a surficial dwelling worm was reduced in the cages rather than elevated in abundance. One possible explanation for this pattern could be competition for surface with the highly abundant Streblospio. Streblospio are relatively small but may crowd the less abundant, larger worms, potentially interfering with its ability to feed or respire.

In unvegetated areas, Streblospio were again most enhanced numerically among the polychaetes (Fig. 19). The dominant amphipod was Ampelisca abdita (Fig. 20), another tube dweller who can be exploited by brown shrimp. Corophium

occurred occasionally in somewhat dense patches. Cores would be dominated by one or the other amphipod, rarely both, and most frequently Ampelisca. Neither Capitella nor Melinna were significantly affected by the removal of predation. The similarity in biomass levels for the natural and no predators treatments may be due, in part at least, to the similarity in abundance of these two large species of worms.

Streblospio benedicti increased to a greater degree in cages on the marsh surface versus those over unvegetated bottom (Figs. 17 and 19). This implies that more of the spionids are potentially lost to predation amid Spartina. An extrapolation leads to the suggestion that marsh surface sediment provides more polychaete biomass to predators than does open water sediment. A salt marsh, then, may be confirmed as more completely satisfying the abundant food requirement of the definition of a nursery area.

Within predator exclusion cages, the infaunal species most likely to be consumed by brown shrimp became the most abundant. There is a chance, however, that changes in substrate caused by the cage itself may be responsible for some of the differences. Cage effects are most often manifest in environments with little structure and significant water movement. The cages add complexity to the area and can dampen currents, allowing for increased settlement of larvae (Hulberg and Oliver 1980). In this case, however, half of my structures were built on the marsh surface, which is already a highly structurally complex area. Further, both vegetated and nonvegetated areas sampled in this

study have very sluggish water movement, due in part to the microtidal aspects of the system. In both cases, it seems somewhat unlikely that cage effects are a significant concern in the currently discussed work (Bell 1980; Kneib and Stiven 1982).

The patterns reported in this dissertation for amphipods are in contrast to those discussed by Nelson (1979b) for pinfish (Lagodon rhomboides) and grass shrimp (Palaemonetes vulgaris) feeding in seagrass beds. My research indicates that in salt marshes tubicolous amphipods are at significant risk of being preyed upon by brown shrimp. In seagrass beds however, amphipod tubes offered a protective advantage to their residents over free living organisms. Further, in the marshes and adjacent open water, tube dwellers responded to a greater degree to the removal of predation than did other amphipods. Once again, in seagrass beds it was the free living forms that significantly increased in number in the absence of predators. Nelson felt that predation was a primary force in determining the abundance and diversity of amphipods in sea grass beds. Contrasts in our results may be related to both differences in the predators and habitats considered. Brown shrimp walk along substrates probing and handling the substrate. They may have a higher success rate at locating cryptic prey than would a more nektonic animal, such as a fish. Grass shrimp may have difficulty in penetrating the substrate to any great degree, as may be true for the white shrimp. While Palaemonetes are known to consume meiofauna (Bell and Coull 1978), removing an active amphipod from its tube

may be beyond the grass shrimp's means. Both salt marshes and seagrass beds are, of course, vegetated, but the variance in plant morphology may necessitate different foraging strategies. In other caging experiments associated with seagrass beds, it has been suggested that predation controls populations of infauna resident in surrounding sand flats but not in the bed itself (Summerson and Peterson 1984). For the salt marsh considered here, it appears that predation may be significant in both the vegetated and nonvegetated habitats. The importance of predation varies, though, as a dominant structuring force between groups of infauna.

Variation in the effects of predation can be significant in the structuring of an infaunal population. In seagrass beds, Leber (1985) studied the effects of feeding by pink shrimp (Penaeus duorarum) and other predators on amphipod communities. He found that predation coupled with microhabitat availability resulted in varying levels of pressure being exerted on the different species of amphipod. This pattern may be replicated in both polychaetes and amphipods in salt marshes, although the species impacted vary. Certain groups, such as surface dwelling polychaetes and tubicolous amphipods, seem to be more greatly affected by predation in a salt marsh system. Selective removal of these forms could both impact abundance and diversity of the community. Further, there appears to be unequal trophic contributions by infaunal groups. The presence of certain

amphipods or polychaetes may play a greater role in local predator productivity than others.

Brown shrimp can be significant predators of infauna, but the degree of significance appears to change with the type of prey and habitat considered. Although not considered here, there is likely to be a seasonal component to the significance as well (Young et al. 1976; Young and Young 1978). Further, brown shrimp are not the only predators of infauna in estuarine areas. During their estuarine residence period, however, they are significantly attracted to the marsh surface with its abundance of polychaetes. It is this area and this potential prey the model most nearly approximated. In open bottom areas, predation may be only one of several important factors that regulate infaunal populations. Overall, predation may define infaunal communities by selectively impacting certain groups, in this case superficial dwelling polychaetes and tubicolous amphipods.

CONCLUSIONS

Penaeus aztecus and Penaeus setiferus are physically similar animals that appear to have very different ecological roles in salt marshes. These differences are manifested in small and large scale differences between their respective life cycles.

Brown shrimp are among the earliest of spring immigrants into estuaries. Their distribution between vegetated and nonvegetated areas directly reflects relative abundances of infauna in those two habitats. When populations of worms are great in both the marsh and open water sediments, the shrimp are equally distributed between the two areas. As open water densities of prey decrease, brown shrimp tend to concentrate on the marsh surface. While described as an omnivore, the brown shrimp relies most heavily on the faunal element of its diet. Previous research has indicated that at least some plant material appears to be necessary, though, to optimize growth rates. Penaeus aztecus effectively removes infauna from natural sediments and grows normally when fed polychaetes (and amphipods to a lesser extent) under laboratory conditions. At feeding rates suggested from laboratory studies, feeding by brown shrimp may influence polychaete populations amid vegetation. For amphipods in vegetation or either group in open bottom areas, however, the factors defining the population may be more complex.

Penaeus setiferus appears in marshes in late spring or early summer when potential infaunal food sources previously available may already be depleted. Once in estuarine areas, white shrimp are very patchy and often are found equally in vegetated and nonvegetated areas. While they, too, are omnivorous, P. setiferus may rely less on the faunal element of its diet than does the brown shrimp. Moreover, the dominant animal component of the white shrimp's diet has yet to be defined. They do not remove infauna from natural sediment to any significant degree, nor do they grow well when fed polychaetes or amphipods in the laboratory. White shrimp do not have the clear linkage to infaunal populations as do brown shrimp. Given that they seem to spend more time swimming than do brown shrimp, Penaeus setiferus may utilize planktonic resources, such as mysids.

Specific feeding requirements for these shrimp may impact their success both locally and between regions. On a small scale, the community structure of an individual salt marsh may affect the penaeids' ability to forage in the area. For brown shrimp, if the infaunal population is dominated by deep-burrowing polychaetes as opposed to surface dwelling species, there may be insufficient food resources to support a large penaeid population. White shrimp, too, probably have an optimum faunal group that may restrict their effective utilization of an area. At present, this group is not known.

Shrimp feeding requirements may, in part, help to explain differences between regions. White shrimp are the numerically

dominant species in the marshes of South Carolina. In Texas salt marshes, by contrast, brown shrimp outnumber other penaeid species including white shrimp. Further, Texas has higher overall densities of shrimp than does South Carolina. The two regions differ greatly in the accessibility of marsh habitat, both through inundation patterns and degree of reticulation. South Carolina may have large amounts of marsh area, but the mesotidal water exchange and relatively solid stands of cordgrass allow shrimp only brief access to vegetated areas. It has been suggested that predation is responsible for the density differences in the two habitats. This may not be the complete answer. South Carolina not only has less shrimp per unit area than Texas, but a different species dominates. These patterns may be a result of feeding differences as well as differential predation pressure. In South Carolina, with restricted marsh access, white shrimp occur in greater densities than other penaeids. In Texas, patchy marshes and a microtidal water exchange allow mobile species greater access to vegetated areas. Brown shrimp, the species more reliant on infauna, is dominant in these marshes. While a variety of factors may be involved, it is tempting to speculate that feeding requirements play a role in this large scale distributional difference.

Penaeus aztecus and Penaeus setiferus belong to two distinct subgroups within the penaeids, the grooved and nongrooved shrimp. Dietary differences observed between the two species may reflect long term patterns indicative of their groups.

Insufficient information exists in the literature to test this theory. While no evidence exists to confirm or refute the idea, the divergences between the species may also have resulted from competition. It would be impossible to tell, however, which aspect of their life history was initially involved.

Brown shrimp and white shrimp superficially appear to be quite similar animals. Through closer examination in this dissertation and through other research, the two species are shown to diverge on a series of interrelated points.

REFERENCES

- Alon, N.C. and S.E. Stancyk. 1982. Variations in life-history patterns of the grass shrimp, Palaemonetes pugio in two South Carolina estuarine systems. Marine Biology 68:265-276.
- Arntz, W.E. 1980. Predation by demersal fish and its impact on the dynamics of macrobenthos. pp. 179-192 In K.R. Tenore and B.C. Coull (eds.), Marine Benthic Dynamics. University of South Carolina Press, Columbia, South Carolina.
- Baxter, K. N. and W. C. Renfro. 1966. Seasonal occurrence and size distribution of postlarval brown and white shrimp near Galveston, Texas, with notes on species identification. Fishery Bulletin 66: 149-158.
- Bell, S.S. 1980. Meiofauna-Macrofauna interactions in a high salt marsh habitat. Ecological Monographs 50: 487-505.
- Bell, S.S. and B.C. Coull. 1978. Field evidence that shrimp predation regulates meiofauna. Oecologia 35: 141-145.
- Bell, S.S. and B.C. Coull. 1980. Experimental evidence for a model of juvenile macrofauna-meiofauna interactions. pp. 179-192 In K.R. Tenore and B.C. Coull (eds.), Marine Benthic Dynamics. University of South Carolina Press, Columbia, South Carolina.
- Biggs, R.B. and L.E. Cronin. 1981. Special characteristics of estuaries. pp. 3-23. In B.J. Neilson and L.E. Cronin (eds.), Estuaries and Nutrients. Humana Press, Clifton, New Jersey.
- Boesch, D.F. and R.E. Turner. 1984. Dependence of fisheries species on salt marshes: the role of food and refuge. Estuaries 7: 460-468.

- Brenchly, G.A. 1981. Disturbance and community structure: an experimental study of bioturbation in marine soft-bottom environments. Journal of Marine Research 39: 767-790.
- Broad, A. C. 1965. Environmental requirements of shrimp. Publications of the Public Health Service, Washington Vol. 999-wp-25: 86-91.
- Camilleri, J.C. and G. Ribí. 1986. Leaching of dissolved organic carbon (DOC) from dead leaves, formation of flakes from DOC, and feeding on flakes by crustaceans in mangroves. Marine Biology 91: 337-344.
- Cammen, L.M. 1979. The macro-infauna of a North Carolina salt marsh. American Midland Naturalist 102: 244-253.
- Chong, V.C. and A. Sasekumar. 1981. Food and feeding habits of the white prawn Penaeus merguensis. Marine Ecology Progress Series 5: 185-191.
- Commuto, J.A. 1982. Importance of predation by infaunal polychaetes in controlling the structure of a soft-bottom community in Maine, USA. Marine Biology 68: 77-81.
- Condrey, R. E., J. G. Gosselink and H. J. Bennet. 1972. Comparison of the assimilation of different diets by Penaeus setiferus and P. aztecus. Fishery Bulletin 70: 1281-1292.
- Cook, H. L. and M. A. Murphy. 1969. The culture of larval penaeid shrimp. Transactions of the American Fisheries Society 4: 751-754.
- Copeland, B. J. and T. J. Bechtel. 1974. Some environmental limits of six Gulf coast estuarine organisms. Contributions in Marine Science 18: 169-204.
- Coull, B. C. 1985. Long-term variability of estuarine meiobenthos: an 11 year study. Marine Ecology Progress Series 24: 205-218.

- Coull, B. C. and M. Palmer. 1984. Field experimentation in meiofauna ecology. Hydrobiologia 118: 1-19.
- Currin, B.M., J.P. Reed, and J.M. Miller. 1984. Growth, production, food consumption, and mortality of juvenile spot and croaker: a comparison of tidal and nontidal nursery areas. Estuaries 7: 451-459.
- Dall, W., B.J. Hill, P.C. Rothlisberg, and D.J. Staples. 1990. The biology of the penaeidae. Advances in Marine Science 27: 1-489.
- Darnell, R.M. 1958. Food habits of fishes and larger invertebrates of Lake Pontchartrain, Louisiana, an estuarine community. Publications of the Institute of Marine Science, University of Texas 5: 353-416.
- Darnell, R. M. 1961. Trophic spectrum of an estuarine community, based on studies of Lake Pontchartrain, Louisiana. Ecology 42: 553-568.
- Darnell, R. M. 1967. Organic detritus in relation to the estuarine ecosystem, pp. 376-382. In G.H. Lauff (ed.), Estuaries. AAAS Publ. 83. Washington, D.C..
- Farfante, I. P. 1969. Western Atlantic shrimps of the genus Penaeus. Fishery Bulletin 67: 461-591.
- Fauchald, K. and P.A. Jumars. 1979. The diet of worms: a study of polychaete feeding guilds. Oceanography and Marine Biology Annual Review 17: 195-284.
- Flint, R. W. and R. D. Kalke. 1985. Benthos structure and function in a south Texas estuary. Contributions in Marine Science 28: 33-53.
- Fry, B. and E.B. Sherr. 1984. $\delta^{13}\text{C}$ measurements as indicators of carbon flow in marine and freshwater ecosystems. Contributions in Marine Science 27: 13-47.

- Gallagher, J. L. 1971. Algal productivity and some aspects of the ecological physiology of the edaphic communities of Canary Creek tidal marsh. Ph.D. Dissertation, University of Delaware, Newark. 120 pp.
- Gleason, D. F. 1986. Utilization of salt marsh plants by postlarval brown shrimp: carbon assimilation rates and food preferences. Marine Ecology Progress Series 31: 151-158.
- Gleason, D. F. and G. M. Wellington. 1988. Food resources of postlarval brown shrimp (Penaeus aztecus) in a Texas salt marsh. Marine Biology 97: 329-337.
- Gleason, D. F. and R. J. Zimmerman. 1984. Herbivory potential of postlarval brown shrimp associated with salt marshes. Journal of Experimental Marine Biology and Ecology 84: 235-246.
- Guillard, R.R.L. 1975. Culture of phytoplankton for feeding marine invertebrates. pp. 29-60. In W.L. Smith and M.H. Chanley (eds.) Culture of Marine Invertebrate Animals, Plenum, New York.
- Gunter, G. 1945. Studies of marine fishes of Texas. Publications of the Institute of Marine Science, University of Texas 1: 1-190.
- Hackney, C.T. and E.B. Haines. 1980. Stable carbon isotope composition of fauna and organic matter collected in a Mississippi estuary. Estuarine and Coastal Marine Science 10: 703-708.
- Haines, E.B. 1977. The origins of detritus in Georgia salt marsh estuaries. Oikos 29: 254-260.
- Haines, E.B. 1979. Interactions between Georgia salt marshes and coastal waters: a changing paradigm. pp. 35-46. In R.I. Livingston (ed.), Ecological Processes in Coastal and Marine Systems, Plenum Press, New York.

- Haines, E.B. and C.L. Montague. 1979. Food sources of estuarine invertebrates analyzed using $^{13}\text{C}/^{12}\text{C}$ ratios. Ecology 60: 48-56.
- Hughes, E.H. and E.B. Sherr. 1983. Subtidal food webs in a Georgia estuary: $\delta^{13}\text{C}$ analysis. Journal of Experimental Marine Biology and Ecology 67: 227-242.
- Hulberg, L.W. and J.S. Oliver. 1980. Caging manipulations in marine soft-bottom communities: importance of animal interactions or sedimentary habitat modifications. Canadian Journal of Fisheries and Aquatic Sciences 37: 1130-1139.
- Hunter, J. 1984. Immunological dietary analysis and diel feeding chronology for Penaeus aztecus Ives and Penaeus setiferus (L.) in tidal creeks of North Inlet, South Carolina. M.S. Thesis, University of South Carolina. Columbia, SC. 66 pp.
- Hunter, J. and R. J. Feller. 1987. Immunological dietary analysis of two penaeid shrimp species from a South Carolina tidal creek. Journal of Experimental Marine Biology and Ecology 107: 61-70.
- Johnson, M.C. and J.R. Fielding, 1956. Propagation of the white shrimp, Penaeus setiferus (Linn.), in captivity, Tulane Stud. Zool., 4: 175-190.
- Jones, R. R. 1973. Utilization of Louisiana estuarine sediments as a source of nutrition for the brown shrimp Penaeus aztecus Ives. Ph.D. Dissertation, Louisiana State University. Baton Rouge, LA. 131 pp.
- Karim, M. 1970. Influence of diet on the feeding behavior, growth, and thermal resistance of postlarval Penaeus aztecus and Penaeus setiferus. Ph.D. Dissertation, Texas A&M University. 94 pp.

- Kent, A.C. and R.W. Day. 1983. Population dynamics of an infaunal polychaete: the effect of predators and an adult-recruit interaction. Journal of Experimental Marine Biology and Ecology 73: 185-203.
- Kneib, R.T. 1984. Patterns of invertebrate distribution and abundance in the intertidal salt marsh: causes and questions. Estuaries 7: 392-412.
- Kneib, R.T. 1985. Predation and disturbance by grass shrimp, Palaemonetes pugio Holthuis, in soft-substratum benthic invertebrate assemblages. Journal of Experimental Marine Biology and Ecology 93: 91-102.
- Kneib, R.T. and A.E. Stiven. 1982. Benthic invertebrate responses to size and density manipulations of the common mummichog, Fundulus heteroclitus, in an intertidal salt marsh. Ecology 63: 1518-1532.
- Knudsen, E.E., W.H. Herke, and J.M. Mackler, 1977. The growth rate of marked juvenile brown shrimp, Penaeus aztecus, in a semi-impounded Louisiana coastal marsh. Proc. Gulf Carib. Fish. Inst. 29th Sess., pp. 144-157.
- Leber, K.M. 1985. The influence of predatory decapods, refuge, and microhabitat selection on seagrass communities. Ecology 66: 1951-1964.
- Levin, L.A. 1982. Interference interaction among tube-dwelling polychaetes in a dense infaunal assemblage. Journal of Experimental Marine Biology and Ecology 65: 107-119.
- Lindner, M. J. and H. L. Cook. 1970. Synopsis of biological data on the white shrimp Penaeus setiferus (Linnaeus) 1767. FAO Fishery Report 57: 1439-1469.
- Lovett, D. L. and D. L. Felder. 1990. Ontogenetic change in digestive enzyme activity of larval and postlarval white shrimp Penaeus setiferus (Crustacea, Decapoda, Penaeidae). Biological Bulletin 178: 144-159.

- Mann, K.H. 1988. Production and use of detritus in various freshwater, estuarine, and coastal marine ecosystems. Limnology and Oceanography 33: 910-930.
- Mayer, M. A. 1985. Ecology of juvenile white shrimp, Penaeus setiferus Linnaeus, in the salt marsh habitat. M.S. Thesis, Georgia Institute of Technology. Atlanta, GA. 62 pp.
- McTigue, T. A. and R. J. Feller. 1989. Feeding of juvenile white shrimp Penaeus setiferus: periodic or continuous? Marine Ecology Progress Series 52: 227-233.
- McTigue, T. A. and R. J. Zimmerman. 1991. Carnivory versus herbivory in juvenile Penaeus setiferus (Linnaeus) and Penaeus aztecus Ives. Journal of Experimental Marine Biology and Ecology 151: 1-16.
- Minello, T. J. and R. J. Zimmerman. 1983. Fish predation of juvenile brown shrimp, Penaeus aztecus Ives: the effect of simulated Spartina structure on predation rates. Journal of Experimental Marine Biology and Ecology 72: 211-231.
- Minello, T. J. and R. J. Zimmerman. 1985. Differential selection for vegetative structure between juvenile brown shrimp (Penaeus aztecus) and white shrimp (Penaeus setiferus), and implications in predator-prey relationships. Estuarine, Coastal and Shelf Science 20: 707-716.
- Minello, T. J., R. J. Zimmerman and E. X. Martinez. 1989. Mortality of young brown shrimp Penaeus aztecus in estuarine nurseries. Transactions of the American Fisheries Society 118: 693-708.
- Nelson, W.G. 1979a. An analysis of structural pattern in an eelgrass (Zostera marina L.) amphipod community. Journal of Experimental Marine Biology and Ecology 39: 231-264.
- Nelson, W.G. 1979b. Experimental studies of selective predation on amphipods: consequences for amphipod distribution and abundance. Journal of Experimental Marine Biology and Ecology 38: 225-245.

- Nelson, W.G. 1981. Experimental studies of decapod and fish predation on seagrass macrobenthos. Marine Ecology Progress Series 5: 141-149.
- Odum, E.P. and A.A. de la Cruz. 1967. Particulate organic detritus in a Georgia salt marsh-estuarine ecosystem, pp. 383-388. In G.H. Lauff (ed.), Estuaries. AAAS Publ. 83. Washington, D.C..
- Pearson, J. C. 1939. The early life histories of some American Penaeidae chiefly the commercial shrimp Penaeus setiferus (Linn.). Bulletin of the United States Bureau of Fisheries 49: 1-73.
- Peterson, C.H. 1977. Competitive organization of the soft-bottom macrobenthic communities of southern California lagoons. Marine Biology 43: 343-359.
- Pomeroy, L. R. 1959. Algal productivity in salt marshes of Georgia. Limnology and Oceanography 4: 386-397.
- Reise, K. 1977. Predation pressure and community structure of an intertidal soft-bottom fauna, pp. 513-519. In B.F. Keegan, P.O. Ceidigh, and P.J.S. Boaden (eds.), Biology of Benthic Organisms. Pergamon Press, New York.
- Rönn, C., E. Bonsdorff, W.G. Nelson. 1988. Predation as a mechanism of interference within infauna in shallow brackish water soft bottoms: experiments with an infauna predator, Nereis diversicolor O.F. Müller. Journal of Experimental Marine Biology and Ecology 116: 143-157.
- Service, S.K., R.J. Feller, B.C. Coull, and R. Woods. 1992. Predation effect of three fish species and a shrimp on macrobenthos and meiobenthos in microcosms. Estuarine, Coastal, and Shelf Science 34: 277-293.
- Shewbart, K. L., W. L. Mies and P. D. Lugwig. 1973. Nutritional requirements of brown shrimp Penaeus aztecus. Texas A&M University Sea Grant Program, TAMU-SG-73-205. 53 pp.

- Sullivan, M. J. and C. A. Moncreiff. 1987. Functional importance of algal productivity in Mississippi salt marshes. Mississippi-Alabama Sea Grant Consortium, Project No. R/LR-15. 103 pp.
- Sullivan, M. J. and C. A. Moncreiff. 1990. Edaphic algae are an important component of salt marsh food-webs: evidence from multiple stable isotope analyses. Marine Ecology Progress Series 62: 149-159.
- Summerson, H.C. and C.H. Peterson. 1984. Role of predation in organizing benthic communities of a temperate-zone seagrass bed. Marine Ecology Progress Series 15: 63-77.
- Suthers, I.M. 1984. Functional morphology of the mouthparts and gastric mill in Penaeus plebejus Hess (Decapoda:Penaeidae). Australian Journal of Marine and Freshwater Research 35: 785-792.
- Teal, J.M. 1962. Energy flow in the salt marsh ecosystem of Georgia. Ecology 43: 614-624.
- Turner, R.E. 1977. Intertidal vegetation and commercial yields of penaeid shrimp. Transactions of the American Fisheries Society 106: 411-416.
- Turner, R.E. 1978. Community plankton respiration in a salt marsh estuary and the importance of macrophytic leachates. Limnology and Oceanography 23: 442-451.
- Venkataramiah, A., G. J. Lakshmi and G. Gunter. 1975. Effect of protein level and vegetable matter on growth and food conversion efficiency of brown shrimp. Aquaculture 6: 115-125.
- Virnstein, R.W. 1977. The importance of predation by crabs and fishes on benthic infauna in Chesapeake Bay. Ecology 58: 1199-1217.
- Weinstein, M. P. 1979. Shallow marsh habitats as primary nurseries for fishes and shell fish, Cape Fear River, North Carolina. Fishery Bulletin 77: 339-357.

- Wenner, E.L. and H.R. Beatty. 1993. Utilization of shallow estuarine habitats in South Carolina, U.S.A., by postlarval and juvenile stages of Penaeus spp. (Decapoda: Penaeidae). Journal of Crustacean Biology 13: 280-295.
- Weymouth, F. W., M. J. Lindner and W. W. Anderson. 1933. Preliminary report on the life history of the common shrimp Penaeus setiferus (Linn.). Fishery Bulletin 14: 1-25.
- Wheeler, R.S., 1968. Culture of penaeid shrimp in brackish-water ponds, 1966-1967. Proc. 22nd Conf. S.E. Assoc. Game Fish. Comm., 5 pp.
- Wiegert, R.G. and B.J. Freeman. 1990. Tidal salt marshes of the southeast Atlantic coast: a community profile. Biological Report 85: 1-17.
- Williams, A. B. 1955. A contribution to the life histories of commercial shrimps (Penaeidae) in North Carolina. Bulletin of Marine Science 5: 116-146.
- Williams, A. B. 1984. Shrimps, Lobsters, and Crabs of the Atlantic Coast of the Eastern United States, Maine to Florida. Smithsonian Institution Press, Washington, D.C. 550 pp.
- Woodin, S.A. 1976. Adult larval interaction in dense infaunal assemblages: patterns of abundance. Journal of Marine Research 34: 25-41.
- Woodin, S.A. 1978. Refuges, disturbance, and community structure: a marine soft-bottom example. Ecology 62: 274-284.
- Wooden, S.A. 1981. Disturbance and community structure in a shallow water sand flat. Ecology 62: 1052-1066.
- Young, D.K., M.A. Buzas, and M.W. Young. 1976. Species densities of macrobenthos associated with seagrasses: a field experimental study of predation. Journal of Marine Research 34: 577-592.

- Young, D.K. and M.W. Young. 1978. Regulation of species densities of seagrass-associated macrobenthos: evidence from field experiments in the Indian River estuary. Journal of Marine Research 36: 569-593.
- Young, J. H. 1959. Morphology of the white shrimp Penaeus setiferus (Linnaeus 1759). Fisheries Bulletin 59: 1-168.
- Zein-Eldin, Z. 1963. Effects of salinity on the growth of post-larval penaeid shrimp. Biological Bulletin 125: 188-196.
- Zimmerman, R. J. and T. J. Minello. 1984. Densities of Penaeus aztecus, Penaeus setiferus, and other natant macrofauna in a Texas salt marsh. Estuaries 7: 421-433.
- Zimmerman, R. J., T. J. Minello, M. C. Castiglione and D. L. Smith. 1990. Utilization of marsh and associated habitats along a salinity gradient in Galveston Bay. NOAA Tech. Memo. NMFS-SEFC-250. 68 pp.
- Zimmerman, R. J., T. J. Minello and J. G. Zamora. 1984. Selection of vegetated habitat by brown shrimp, Penaeus aztecus, in a Galveston Bay salt marsh. Fisheries Bulletin 82: 325-336.